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# ILLINOIS BIOLOGICAL MONOGRAPHS

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EDITORIAL COMMITTEE

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JOHN THEODORE BUCHHOLZ

FRED WILBUR TANNER

HARLEY JONES VAN CLEAVE



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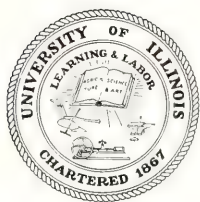
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JOHN THEODORE BUCHHOLZ

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HARLEY JONES VAN CLEAVE



THE MORPHOLOGY, TAXONOMY, AND  
BIONOMICS OF THE NEMERTEAN  
GENUS CARCINONEMERTES

WITH FOUR PLATES AND ONE MAP

BY  
ARTHUR GROVER HUMES

CONTRIBUTION FROM THE DEPARTMENT OF ZOOLOGY

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Dr. R. R. Kudo of the University of Illinois has translated from the Japanese a paper by Takakura, which will, when republished in part, be of great interest to students of nemerteans. For this translation the writer is particularly grateful, because without it much of the taxonomic and morphological material in this study would be incomplete.

Dr. H. J. Van Cleave, under whose direction this study has been made, has offered his friendly encouragement and criticism throughout the work.

## INTRODUCTION

ALTHOUGH all animals at some time in their life histories come in contact with other animals, only a relatively small number become so intimately associated with other species that the latter change from an incidental part of the environment to become an indispensable element of it. The innumerable varieties and degrees of intimacy between animals of different species, extending all the way from the condition of free life to the most dependent type of endoparasitism, defy exact classification. Great interest is attached to animals which live in relationships with each other intermediate to free-living and parasitic ways of life. The morphological modifications present in animals of these various types of associations (commensalism, symbiosis, inquilinism, phoresy, ectoparasitism, etc.) illustrate forcibly the presence of evolutive forces in living cells and the influence of the environment. However, as Caullery (1922) pointed out, the random diversity of the deformations in such animals shows that the evolutive changes are conditioned by the intrinsic properties of the living forms. Our knowledge of the expression of forces at work in animal evolution has been increased by observations on the morphology of animals which are to a greater or lesser degree dependent on individuals of other species. Accurate and detailed information on many groups, however, is still lacking.

Very little is known about those nemertean worms which live in close associations with other animals. Some authors have even been led to make gross misstatements concerning them. Parker and Haswell (1910, p. 296) stated that "one nemertean lives *in the interior* of a crustacean and is probably a true parasite" (*italics mine*). In reality the nemertean referred to lives only as an ectohabitant on the external surface of the exoskeleton. The best known genus of nemerteans which is not free-living is *Malacobdella*, a form which inhabits the mantle cavities of various lamellibranchs. Even for this genus, however, our understanding of the taxonomy, distribution, life history, and host relationships is only fragmentary. Likewise, the genus *Carcinonemertes*, the members of which are ectohabitants of crabs, has been to date much neglected. Further studies on the genus *Carcinonemertes* seemed to the writer to be necessary if only because of the rarity of parasitic and commensal species in the phylum Nemertea. Moreover, a knowledge of the form and function of these animals may eventually be useful in interpreting the phylogenetic evolution of parasitism in the group.

Preliminary observations on *Carcinonemertes* at Grand Isle, Louisiana, and a survey of the previous literature on the genus indicated that several lines of investigation needed to be carried out. In the first place, no adequate description of *Carcinonemertes carcinophila* (Kölliker), the



first species to be described and the type species, existed in the literature. Secondly, although Takakura (1910) mentioned a unique dorsal duct in male specimens of *Carcinonemertes mitsukurii* Takakura, his work, having gone unnoticed by other students of the nemerteans because of its publication in Japanese, needed to be made generally available for study. Especially was this true since a similar dorsal duct was found by the writer in *C. carcinophila*. Because of the uniqueness of the dorsal duct the writer felt that a detailed description of the duct as it exists in the genus *Carcinonemertes* should be given. In the third place, the life history of *C. carcinophila* could now, with the information given by Churchill (1919) and Gray and Newcombe (1939) regarding the life history of the host crab and with the data collected by the writer, be interpreted more fully. In the fourth place, the writer found that by collecting specimens of *Carcinonemertes* from the egg masses of crabs available in museum collections, new data on the distribution of the genus and the various species of crabs infested could be collected. Lastly, taxonomic considerations, involving the description of a new species and a new variety and the diagnosis of the family Carcinonemertidae, demanded a restudy of the genus. Investigations along these five principal lines have been undertaken, and the results are given in the following pages.

#### MATERIALS AND METHODS

THE WORMS used in this study came from two sources. The specimens of *C. carcinophila imminuta* from Grand Isle, Louisiana, were collected alive by the writer during the summers of 1939 and 1940. All other specimens were obtained from the egg masses of ovigerous crabs in the collections of the Museum of Comparative Zoology, Cambridge, Massachusetts, and the United States National Museum, Washington, D. C.

The crabs were obtained at Grand Isle by an otter trawl, by minnow seines, or by hand, and brought into the laboratory before examination for worms was made. Ovigerous crabs were kept in sea water until they could be examined. In this way most of the worm eggs and larvae and immature worms remained in the egg masses in good condition. The non-ovigerous crabs were usually left without water, since in this way they survived better in the relatively high temperatures of the laboratory. In no case did examination occur later than twelve hours after capture.

The crab gills and egg masses if present were removed and placed in separate finger bowls of sea water. Most of the worms which were in capsules between the gill lamellae left the gills within a few hours and congregated on the side of the dish farthest from the source of light. There they could be picked up in a pipette and transferred to clean sea water or to fixative. The transfer had to be made quickly or the worms

adhered to the inside of the pipette. The egg cords of the nemerteans were picked off the egg masses either with the aid of a binocular or without magnification after the eye had become accustomed to their appearance. The free-swimming larvae left the egg masses in a few hours and collected on the side of the finger bowl nearest the source of light, where they were pipetted off into another dish. Very young worms were often found crawling among the debris on the bottom of the dish and along the sides. Mature females were recognized by their relatively greater length and reddish coloration. Mature males, on the other hand, were found to be shorter and whitish rather than red.

Before making measurements of the live worms the specimens were usually first anaesthetized by dropping a few crystals of chloretone into the dish or by placing the dish in a closed chamber with chloroform fumes.

Most of the worms were fixed in either Schaudinn's or Bouin's fluid. The live worms were studied either whole or by maceration. Vital stains, including Bismarck brown, neutral red, methylene blue, and Nile blue sulphate, were useful in accentuating some details of the anatomy. Orange G was especially useful in staining the basis. Nearly all the observations and measurements of the minute structures were made under an oil immersion objective and a 10x ocular.

Many of the worms recovered from crabs in museum collections had been in 70 to 80 per cent alcohol for years. One collection from *Ovalipes ocellatus* (Herbst) had been immersed thus for 89 years. Nearly all of these worms were still inside their mucous sheaths. It was found that with ordinary dehydration in ethyl alcohol and clearing in xylol the worms became very brittle and sectioned poorly. The following technique was then adopted, after experimentation showed that it produced usable sections, even though the worms had been poorly fixed:

50% ethyl alcohol.....	2 hours
35% ethyl alcohol.....	2 hours
35% ethyl alcohol + 2 drops of Labarraque's solution.....	10 minutes
50% ethyl alcohol.....	2 hours
5 cc HOH + 4 cc ethyl alcohol + 1 cc n-butyl alcohol.....	2 hours
3 cc HOH + 5 cc ethyl alcohol + 2 cc n-butyl alcohol.....	2 hours
1.5 cc HOH + 5 cc ethyl alcohol + 3.5 cc n-butyl alcohol.....	3 hours
0.5 cc HOH + 4 cc ethyl alcohol + 5.5 cc n-butyl alcohol.....	5 hours
2.5 cc ethyl alcohol + 7.5 cc n-butyl alcohol.....	7 hours
n-butyl alcohol (undiluted).....	10 hours
change of n-butyl alcohol.....	10 hours
n-butyl alcohol + paraffin at melting point (1:1).....	10 hours
paraffin slightly above melting point.....	2 hours
change of melted paraffin.....	30 minutes

The worms were sectioned 10  $\mu$  in thickness and mounted in the usual manner. At first, safranin followed by fast green as a counterstain was used to stain the sections. By this technique the basis and the nuclei were



stained red, while the fast green colored the basement membrane and the cytoplasm green. However, because of the poor fixation these two stains did not stain the tissue evenly. A more satisfactory stain was Heidenhain's iron haematoxylin, which stained the basis and the nuclei black. The muscle fibers were stained a dark gray by this technique, although here, as with the safranin and fast green, the stain did not color the tissue evenly. Although the contents of the gland cells stained a light pink with safranin, they were unstained with the iron haematoxylin.

The live worms, after being fixed, were washed free of the fixing agent, dehydrated in increasing concentrations of ethyl alcohol, and cleared before embedding in xylol or in cedar oil. The latter clearing agent was found to be far superior, in that it preserved the contents of the intestine, the ocelli, and the cellular details much better. These worms were cut from 4  $\mu$  to 10  $\mu$  in thickness. The most convenient thickness, in respect to ease in cutting and usefulness in identifying structures, was 7  $\mu$ . The sections were stained with safranin and fast green, as mentioned above, with Delafield's haematoxylin, Heidenhain's iron haematoxylin, or rarely with Mallory's phosphotungstic acid haematoxylin. Methylene blue stained only the mucus in the submuscular and cephalic glands. Sections stained with methylene blue and counterstained with eosin showed bright blue glands against a pink background. Feulgen's nucleal reaction, when used on the sectioned Schaudinn-fixed material, was useful in identifying nuclei. In this case fast green was used as a counterstain against the red nuclei.

A few whole mounts stained with Delafield's haematoxylin were prepared, but were too opaque to be of much use.

*CARCINONEMERTES CARCINOPHILA* (KÖLLIKER)  
VAR. *CARCINOPHILA* (KÖLLIKER)

HISTORICAL ACCOUNT

DURING the voyage of the *Astrolabe* in the years 1826-1829, Quoy and Gaimard (1833) found in a barnacle at Amboina a nemertean which they named *Borlasia quadripunctata*. This slender, slightly flattened worm was about two inches long and white, except for two longitudinal brown lines on the dorsal side, the space between being yellow. The head was obtuse, a little indented in front, with no sign of separation from the body. On the dorsal side of the head there were four round, black spots. The mouth was a long terminal slit. From this brief description Coe (1902a) thought it probable that the worm belonged to the genus *Tetrastemma*. No one else has since found such a worm.

This record constitutes the earliest mention in the literature of a crustacean and a nemertean living in any kind of an association.

It was not until 1845 that a nemertean living on crabs was discovered. Kölliker (1845) found six nemerteans living on the egg masses of a small crab at Messina, Sicily. These he named *Nemertes cartinophilos*, giving the following description: "Länge 1-3 Linien. Farbe blassorange. Augen zwei, elliptisch. Darmanhänge kurz, zahlreich. Rüssel sehr kurz, mit einem styletartigen Zahn von 0.013''' versehen. Körper der Samenfäden 0.009''' lang." Von Siebold (1850, p. 382) referred very briefly to Kölliker's species as *Nemertes carcinophilos*, changing the "t" to a "c" to correct an obvious misprint. Modern writers have used the corrected spelling, in accordance with Article 19 of the International Rules of Zoological Nomenclature.

Van Beneden (1861) described a nemertean, *Polia involuta*, which he considered to be a new species, evidently unaware that Kölliker had sixteen years before described the same worm as *Nemertes cartinophilos*. Van Beneden later (1876, pp. 46 and 81) pointed out the priority of Kölliker's name. Van Beneden's description is rather short and contains little that is not much better shown by later authors, especially McIntosh and Coe. His description of the embryology is the first to be found in the literature on the genus Carcinonemertes. The worm has a direct type of development, with no special larval stages such as the pilidium or the larva of Desor. The fertilized and developing eggs are placed in rows in mucous sheaths, much like those in which the adults live, but without the flagstone-like pieces on the surface. The embryo develops cilia before leaving the egg case. The free-swimming ciliated larva has an anterior, and sometimes also a posterior, flexible cirrus or filament which whips about as the larva swims. The skin becomes more and more distinct, while the yolk material passes to the posterior half of the larva to take part in the formation of the intestine. Two minute ocelli are present on the larva. Van Beneden stated that the long filaments at the ends of the larva are shed, and possibly also the entire ciliated covering, though the latter point is not clear. The larva in its shedding process was compared with the miracidium of the Trematoda or the hexacanth of the Cestoda. This comparison is not a good one, for, as will be seen later, the larva of Carcinonemertes is provided with rudiments of nearly all the adult organs, except possibly the gonads.

In 1862, Diesing listed *Cephalothrix involuta* (Van Beneden), which he indicated to be identical with *Polia involuta* Van Beneden, and also *Nemertes carcinophila* Kölliker, not recognizing the synonymy of the two names.

Eight years after Van Beneden's description of *Polia involuta*, McIntosh (1869) described in greater and more exact detail its anatomy and



development. McIntosh was aware of Kölliker's work, since he referred after *Polia involuta* Van Beneden in a footnote to *Nemertes carcinophilus* Kölliker. No reason was given for continuing to use Van Beneden's name, when the worm described by the latter as *P. involuta* was clearly the same species as *N. cartinophilus* Kölliker 1845. The areolar sheaths attached to the bases of the abdominal appendages of ovigerous female crabs, *Carcinides* (= *Carcinus*) *maenas* (Linnaeus), were described and a good description of the proboscis and head region given. The absence of the proboscis sheath and the rhynchocoel with its fluid was mentioned briefly. His description of the anterior region and the development of the young worms is accompanied by drawings which, for the first time, indicate something of the histology of the proboscis, the whole head, the early egg, and the ciliated free-swimming larva.

McIntosh (1873-1874) wrote an extensive monograph on nemerteans published by the Ray Society of London. In this the name *Polia involuta* Van Beneden was discarded in favor of *Nemertes carcinophila* Kölliker. Included in the monograph is a synonymy and brief description of this species, which he found on *Carcinides* (= *Carcinus*) *maenas* (Linnaeus) at St. Andrews, Scotland. His remarks on the internal anatomy and development were repeated verbatim from his 1869 paper. In addition to the 1869 figures there is a colored figure of the whole worm. The drawing of the anterior region of the body has the blood vessels shown in blue.

Another nemertean from a decapod crustacean at Messina, Sicily, was reported by Dieck (1874). This worm, named by him *Cephalothrix galathea*, occurred in the egg masses of an anomuran, *Galathea strigosa* Linnaeus. Dieck apparently knew nothing of Kölliker's previous work. Coe (1902a) has critically evaluated this species and concluded that it very probably is synonymous with *Nemertes carcinophila* Kölliker. The general body form (size, shape, color, ocelli, absence of cephalic furrows and cerebral sense organs), the eggs and developmental stages, the occurrence in the same locality (Messina), and the presence of internal fertilization all show great similarity to Kölliker's worm. Bürger (1897-1907) disagreed with Coe's interpretation and argued that Dieck's species should be considered distinct, inasmuch as it was described as having the mouth behind the brain, a proboscis without a stylet, and the lateral nerve cords enclosed in the body muscle layer. The writer feels that the decision regarding the specific identity of these two worms should be postponed until additional specimens of *Cephalothrix galathea* (if such a species exists) can be obtained.

Willemoes-Suhm (1874) found a parasitic nemertean on the ventral side of the abdomen of a Gulf-weed crab, *Planes* (= *Nautilograpsus*) *minutus* (Linnaeus), between the Azores and Bermuda. This was de-

scribed as small, brownish, two millimeters in length, with a very short proboscis. Two pairs of eyes were present, the second only punctiform. In his figure 4, Willemoes-Suhm showed two accessory stylet pouches, each having two or three minute stylets. These were not mentioned in the text. This worm was later called *Prostoma suhmi* by Bürger (1897-1907). Since the specimens of this worm were lost during the voyage of the Challenger, Hubrecht (1887), while studying the nemerteans collected on that famous voyage, was unable to determine anything further. It is possible that the worm was a free-living species which accidentally was present on the abdomen of the crab. When a batch of Sargassum weed is hauled up out of the water to be examined, many of the animals are apt to be uprooted and transplanted to unnatural situations.

The embryology of the Nemertea was considered by Barrois (1877) in some detail. He concluded that two chief types are present, the one comprising the pilidium and the larva of Desor, and the other the direct development and the so-called "planula." The development of *Polia carcinophila* (Kölliker) (= *Nemertes carcinophila* Kölliker) was shown to be of the direct type. The larva is a nemertean already formed and has nothing comparable to a "planula." The development of this species resembles closely that of *Amphiporus lactifloreus*. The chief difference is that the young nemertean when hatched, instead of adopting the adult way of life, starts to swim freely in the water. The differentiation of the musculature occurs in *P. carcinophila* before the peripheral epithelium is separated completely from the white deutoplasmic mass in the center of the embryo. Barrois was unable to tell whether the free-swimming larva sheds its skin before changing from a swimming to a crawling way of life. Van Beneden (1861) for *Polia involuta* (= *Nemertes carcinophila*) and Dieck (1874) for *Cephalothrix galathea* both affirmed that the ciliated skin is shed, but McIntosh (1869) denied this. According to Barrois the newly hatched larva shows a clearly indicated proboscis, a structure which McIntosh mistook for the esophageal region. Even in the unhatched embryos a vague rudiment of the proboscis may be visible. In the young larva the proboscis is a hollow structure but unarmed. The body is covered with cilia and there are long apical flagella at both ends. As the worm grows, the armature of the proboscis appears. There is no proboscis sheath, the proboscis floating free in the cavity of the body above the intestine. The lateral organs are absent.

Carus (1885) placed Dieck's species in the genus *Carinella* as *Carinella galathea* (Dieck), and stated that it is perhaps synonymous with *Nemertes carcinophila* Kölliker. He listed the latter species separately however. *Polia involuta* Van Beneden he regarded as a synonym of *Nemertes carcinophila* Kölliker.

Hubrecht (1887) quoted from the journal of Willemoes-Suhm a brief



description of the worm from *Planes minutus* (Linnaeus). However, this description contains no information beyond that given in the 1874 paper, except that the stylet lies just behind the ganglia, which are large. Braun (1888) mentioned *Nemertes carcinophila* K  lliker and *Cephalothrix galathea* Dieck (which he held to be separate species) and summarized some of the previous work on these worms.

Female specimens of *Xantho floridus* Mont. at Concarneau, France, were found by Giard (1888) to be infested with a small nemertean, which he called *Polia xanthophila*, giving no description or diagnosis of any kind. Ovigerous specimens of *Carcinides* (= *Carcinus*) *maenas* (Linnaeus) were infested at Wimereux (about 300 miles northeast of Concarneau) with a worm which Giard identified as *Polia involuta* Van Beneden (= *Nemertes carcinophila* K  lliker). It is very probable that the worms in the two localities were the same species. In 1890 Giard again recorded the presence of *Nemertes carcinophila* K  lliker at Wimereux, and noted its synonymy with *Polia involuta* Van Beneden. He found the worms very common in the spring on the eggs of *Carcinides* (= *Carcinus*) *maenas* (Linnaeus). Joubin (1890) found *Nemertes carcinophila* K  lliker on *Carcinides maenas* at Roscoff, France. A male and a female were often found in the same mucous sheath and sometimes were folded two or three times in respect to length. He did not find Dieck's species, which he regarded as *Carinella galathea* (Dieck), although the host, *Galathea strigosa* Linnaeus, was common there.

Van Beneden (1883) recorded *Polia involuta* Van Beneden (= *Nemertes carcinophila* K  lliker) at Ostende, Belgium.

While making a survey of the nemerteans of Plymouth Sound, England, Riches (1893-1895) did not find *Nemertes carcinophila*, although he examined ovigerous *Carcinides maenas*. He cited McIntosh as having stated that these worms had been found only at Messina, Sicily, and on the coast of Belgium, not in England. He was evidently unaware of the fact that McIntosh had found *Nemertes carcinophila* at St. Andrews, Scotland, in 1869. Riches also examined several ovigerous *Galathea strigosa* Linnaeus, but found none of Dieck's *Cephalothrix galathea*.

In his famous monograph of the nemerteans of the Gulf of Naples, B  rger (1895) mentioned *Eunemertes carcinophila* (K  lliker) and cited McIntosh's (1873-1874) description and figures. Attention was called by him to the fact that McIntosh, Pl. 12, fig. 14, showed the main stylet half as long as the basis.

Richard (1899) listed four species of nemerteans found on Crustacea. They were *Eunemertes carcinophila* (K  lliker), *Eunemertes xanthophila* (Giard), *Carinella galathea* (Dieck), and *Tetrastemma fuscum* Willemoes-Suhm (= *Prostoma suhmi* B  rger).

A nemertean on crabs in North America was reported in the literature for the first time by Coker (1901). He mentioned that among the inhabitants of the gill chambers of *Callinectes sapidus* Rathbun at Beaufort, North Carolina, there were "vorticellid colonies and acinetid Protozoa, Polyzoa—ectoproctous and endoproctous—nemerteans, etc." This is also the first record of any nemerteans from the blue crab *Callinectes sapidus*. No details regarding these nemerteans were given, although they were undoubtedly *Carcinonemertes carcinophila* (Kölliker), since this species has since been found in the same locality.

In 1902, Coe published a paper on the nemertean parasites of crabs, in which he summarized, evaluated, and reorganized the previous work on the group. In it, a new genus, *Carcinonemertes*, and a new species, *Carcinonemertes epialti*, were described and a redescription of *Carcinonemertes carcinophila* (Kölliker) was given. Coe mentioned that Professor J. P. McMurrich in correspondence stated that he had found nemerteans among the egg masses of the lady crab, *Ovalipes* (= *Platyonichus*) *ocellatus* (Herbst), in July, 1889. He pointed out that this was the first observation of a nemertean living on a crab in this country, though no definite locality was given. This unpublished note preceded Coker's paper in time.

Coe's paper (1902a) constitutes the first piece of work ever done on New World nemerteans living on crabs. He found on *Platyonichus ocellatus* (Herbst) (= *Ovalipes ocellatus ocellatus* (Herbst)) at Cape Cod, Massachusetts, a nemertean which he regarded as identical with the previously described European species, *Nemertes carcinophila* Kölliker. For this he erected his new genus, inasmuch as the anatomical structures were so decidedly different from those of *Eunemertes* in which the worm had been placed by Joubin and by Bürger. Some details regarding the development and life history of the genus were included in the paper. In the same year Coe (1902b) republished his generic description of *Carcinonemertes* and rediagnosis of *C. carcinophila* (Kölliker). In 1904b (pp. 150-154) and 1905a (pp. 230-233) Coe repeated his original (1902a) descriptions of the genus *Carcinonemertes*.

Bürger (1897-1907), on page 530 of his extensive discussion of the Nemertea, mentioned *Carcinonemertes carcinophilon* (Kölliker), using the ending *-on* instead of either the original *-os* or the *-a* of later authors.

In their list of the fauna of Woods Hole (1913), Sumner, Osburn, and Cole mentioned (p. 591) *Carcinonemertes carcinophila* (Kölliker) from Nobska Point, Katama Bay, and Nememsha Bight, Massachusetts. A new family name, *Carcinonemertidae*, was used, evidently for the first time and without diagnosis of any kind. Most other authors since Coe's description of the genus have placed it in the family *Emplectonematidae* Bürger (1904).

Shipley (1926) in a brief discussion of the parasitic nemerteans suggested that those living on Crustacea, like *Malacobdella*, which lives in the mantle cavities of marine clams, have "an organ of attachment, a sucker, a feature unknown in the free-living forms . . . the alimentary canal has no lateral pouches, but as a compensation it is longer than the body, and coiled." It is easy to see that he was here describing *Malacobdella* and not *Carcinonemertes*. The description created an erroneous idea of the so-called parasitic nemerteans as a group.

Pearse (1932) found in the gill lamellae of *Bathynectes superba* (Costa), taken 20 miles south of Tortugas, Florida, in 155 fathoms, worm-like parasites containing two lateral, pigmented spots near the anterior end. *Portunus spinicarpus* Stimpson from the Gulf Stream in 60 fathoms of water was reported by the same author to be infested in the gill lamellae by "worms with the lateral eye spots." These were verified as *Carcinonemertes carcinophila* (Kölliker) by Dr. A. S. Pearse and reported as such in conversation with the writer in Philadelphia, Pennsylvania, on January 1, 1941.

In correspondence of June 16, 1940, Dr. Wm. E. De Turk stated that he had found nemerteans (later identified by Dr. W. R. Coe as *C. carcinophila*) on *Portunus spinimanus* Latreille, *Ovalipes ocellatus ocellatus* (Herbst), *Ovalipes ocellatus guadulpensis* (Saussure), *Callinectes sapidus* Rathbun, and *Callinectes ornatus* Ordway, all at Beaufort, North Carolina. He reported finding larvae (by which he no doubt meant immature worms) on both sexes of the hosts.

#### SPECIFIC DESCRIPTION

The synonymy of *Carcinonemertes carcinophila carcinophila* (Kölliker, 1845) Coe, 1902, is as follows:

- 1845 *Nemertes cartinophilos* Kölliker. Verhandl. Schweiz. Naturf. Gesellsch. 29: 86-98.
- 1850 *Nemertes carcinophilos* Kölliker. Von Siebold, Arch. f. Naturgesch. 16:351-468.
- 1861 *Polia involuta* Van Beneden. Mem. Acad. roy. Sci. Belg. 32:1-56.
- 1862 *Cephalothrix involuta* (Van Beneden). Diesing, Sitzb. kais. Akad. Wiss. Wien 45:191-318.
- 1862 *Nemertes carcinophila* Kölliker. Diesing, ibid.
- 1869 *Nemertes carcinophilus* Kölliker. McIntosh, Trans. Roy. Soc. Edinb. 25:305-433.
- 1869 *Polia involuta* Van Beneden. McIntosh, ibid.
- 1873-1874 *Nemertes carcinophila* Kölliker. McIntosh, Monogr. Brit. Annelids, part 1, pp. 1-213.
- 1874 ?*Cephalothrix galathea* Dieck. Jen. Zeitschr. f. Naturw. 8:500-520.
- 1877 *Polia carcinophila* (Kölliker). Barrois, Ann. Sci. nat. (6) 6:1-232.
- 1883 *Polia involuta* Van Beneden. Van Beneden, E., Bull. Acad. roy. Belg. (3) 6:458-483.
- 1885 ?*Carinella galathea* (Dieck). Carus, Prodrum Faunae Mediterraneae, vol. 1.
- 1888 *Polia xanthophila* Giard. Bull. sci. Fr. et Belg. 19:492-513.



- 1890 ?*Carinella galathea* (Dieck). Joubin, Arch. Zool. exp. et gén. (2) 8:416-602.  
 1890 *Eunemertes carcinophila* (Kölliker). Joubin, *ibid.*  
 1895 *Eunemertes carcinophila* (Kölliker). Bürger, Fauna u. Flora d. Golfes von Neapel 22:1-743.  
 1895 *Emplectonema carcinophila* (Kölliker). Verrill, Trans. Conn. Acad. Arts and Sci. 9:523-534.  
 1899 *Eunemertes xanthophila* (Giard). Richard, Arch. de Parasitol. 2:548-595.  
 1902 *Carcinonemertes carcinophila* (Kölliker). Coe, Amer. Naturalist 36:431-450.  
 1902 *Carcinonemertes carcinophila* (Kölliker). Coe, Zool. Anz. 25:409-414.  
 1904 *Emplectonema carcinophilum* (Kölliker). Bürger, in Schulze, "Das Tierreich," part 20, pp. 1-151.  
 1897-1907 *Carcinonemertes carcinophilum* (Kölliker). Bürger, in Bronn, "Klass. u. Ord. des Tierreichs," 4 (suppl.):1-542.

Kölliker's original description is very brief. In translation it is as follows: "Length 1-3 lines. Color pale orange. Two elliptical eyes. Intestinal pouches short, numerous. Proboscis very short, provided with a stylet-like tooth 0.013". Bodies of the spermatozoa 0.009" long. Six of these worms of different sizes were found at Messina in the egg masses of a small crab." Converting the measurements in lines (see Behrens, 1908) to the metric system now used, the length is 2.1 to 6.3 mm, the stylet-like tooth is 27.5  $\mu$ , and the bodies of the spermatozoa are 19  $\mu$ .

Later writers (Van Beneden 1861, McIntosh 1873-1874, and Bürger 1895) have redescribed the worm under various names (see synonymy above). The rediagnosis of the species by Coe (1902a) is the most exact. This in brief is as follows: The body is slender, 6-15 mm long when on the gills and 20-70 mm when sexually mature. The color is yellowish orange, pale reddish, rose pink, or bright brick red. The posterior proboscis chamber is very small and rounded. The central stylet lies immediately posterior to the brain, when the worm is in the ordinary states of contraction. The slender basis measures about 25-30  $\mu$  in length by 6-8  $\mu$  in average diameter. The central stylet is about 8-12  $\mu$  long, or about  $\frac{1}{3}$  to  $\frac{1}{2}$  the length of the basis. The worm lives on the gills when young, migrating to the egg masses where it reaches sexual maturity.

Van Beneden (1861) gives no diagnostic information which is not better given by Coe. On Pl. III there are figures of the head region, the eggs, and the free-swimming larvae. In these the basis and stylet are not distinguished, but are drawn as one structure. The "everted proboscis" apparently is the esophagus.

McIntosh (1873-1874) has little to add. He gives figures of the whole worms (in color), on Pl. I, fig. 5; the proboscis on Pl. XII, fig. 14; the head region on Pl. XIV, fig. 4; the ovum on Pl. XVI, figs. 18, 19, and 20; and the ciliated larva and spermatozoa on Pl. XVII, figs. 7 and 9. The stylet apparatus in Pl. III, fig. 14, has the ratio of stylet to basis of 0.543.

Bürger (1895) stated that the mucous sheaths are 8-12 mm in length, and that the males and females are of different sizes, the male worms

TABLE 1.—MEASUREMENT (IN MICRONS) OF STYLET APPARATUS OF *Carcinonemertes carcinophila* (KÖLLIKER) MADE BY COE IN NEW ENGLAND

Length of Basis	Length of Stylet	S:B Ratio
25	8	0.320
19	6	0.316
22	7	0.318
30	12	0.400
23	9	0.390

being 4-5 cm and the females 3 cm in length. This is the exact reverse of the condition found by the writer in other species of the genus and in the new variety to be described below, and may possibly be a *lapsus calami* on Bürger's part.

In correspondence with the writer (November 8, 1940) Dr. Coe gave the following additional figures, shown in Table 1, regarding individuals of *Carcinonemertes carcinophila* (Kölliker) in New England which he studied.

Takakura's duct, to be described in detail below, is present in this species. In structure it is similar to that to be described in *Carcinonemertes carcinophila* var. *imminuta*.

Cephalic muscle fibers (cf. fig. 9), similar to those to be described below for the new variety, are present in the head region, especially along the sides of the rhynchodaeum.

The mucous sheath of one of the worms recovered from the egg mass of a specimen of *Ovalipes ocellatus* (Herbst) in the Museum of Com-

TABLE 2.—MEASUREMENTS OF *Carcinonemertes carcinophila* (KÖLLIKER) FROM NEW ENGLAND

Sex	Length (mm)	Diameter (mm)	Basis ( $\mu$ )	Stylet ( $\mu$ )	S:B Ratio	Middle Chamber ( $\mu$ )	Posterior Chamber ( $\mu$ )
Male.....	3.0	0.385	23 x 6.5	...	.....	32 x 28	63 x 49
Male.....	3.0	0.420	.....	...	.....	30 x 27	52 x 43
Male.....	1.5	0.280	24 x 6.0	8.5	0.354	30 x 25	60 x 40
Female.....	3.0	0.420	23 x 6.0	...	.....	42 x 32	77 x 53
Male.....	2.5	0.490	.....	...	.....	30 x 31	60 x 42
Male.....	3.0	0.350	24 x 6.5	8.0	0.333	32 x 28	.....
Male.....	2.5	0.315	23 x 6.5	...	.....	39 x 30	65 x 45
Averages.....	2.6	0.380	23.5 x 6.3	8.3	0.344	34 x 29	63 x 48

parative Zoology is shown in fig. 11. Only a few scattered small lapilli are present.

The outline of the basis, drawn from sectioned material, is shown in fig. 27.

The measurements of the worms taken from crabs in the Museum

TABLE 3.—THE DISTRIBUTION OF *Carcinonemertes carcinophila* (KÖLLIKER)

Host	Locality and Collector	Name Given
Galatheidæ		
<i>Galathea strigosa</i> L. . . . .	Messina, Sicily; Dieck, 1874	<i>Cephalothrix galatheae</i>
Portunidæ		
<i>Carcinides maenas</i> (L.) . . .	Ostende, Belgium; Van Beneden, 1861 and 1883	<i>Polia involuta</i>
	Roscoff, France; Joubin, 1890	<i>Nemertes carcinophila</i>
	St. Andrews, Scotland; McIntosh, 1873-1874	<i>Nemertes carcinophila</i>
	Wimereux, France; Giard, 1888 and 1890	<i>Nemertes carcinophila</i>
<i>Callinectes sapidus</i> R. . . .	Beaufort, N. Carolina; Coker, 1901	"Nemertean"*
	Beaufort, N. Carolina; De Turk, in correspondence	<i>Carcinonemertes carcinophila</i>
<i>Callinectes ornatus</i> O. . . .	Beaufort, N. Carolina; De Turk, in correspondence	<i>Carcinonemertes carcinophila</i> *
<i>Portunus spinimanus</i> L. . .	Beaufort, N. Carolina; De Turk, in correspondence	<i>Carcinonemertes carcinophila</i> *
<i>Ovalipes ocellatus</i> (H.) . . .	North Dennis, Mass., and other regions south of Cape Cod; Coe, 1902a	<i>Carcinonemertes carcinophila</i>
	Nobska Point, Katama Bay, Nememsha Bight, Woods Hole region, Mass.; Sumner, Osburn, and Cole, 1913	<i>Carcinonemertes carcinophila</i>
	Beaufort, N. Carolina; De Turk, in correspondence	<i>Carcinonemertes carcinophila</i> *
	Buzzard's Bay, Mass.; M.C.Z. 5447	<i>Carcinonemertes carcinophila</i>
	Provincetown, Mass.; M.C.Z. 5444	<i>Carcinonemertes carcinophila</i>
<i>Ovalipes ocellatus gadulpensis</i> (Saussure) . . .	Beaufort, N. Carolina; De Turk, in correspondence	<i>Carcinonemertes carcinophila</i> *
Xanthidæ		
<i>Xantho floridus</i> Mont. . . . .	Concarneau, France; Giard, 1888	<i>Polia xanthophila</i>
"Small crab" . . . . .	Messina, Sicily; Kölliker, 1845	<i>Nemertes cartinophilos</i>

\*These worms may be referable to the variety *imminuta* to be described below.



of Comparative Zoology (*Ovalipes ocellatus* (Herbst), M. C. Z. Nos. 5444 and 5447) are shown in Table 2. The blank spaces appear because in those instances the section was cut at such a plane that accurate measurement of the structure involved was impossible.

#### GEOGRAPHICAL DISTRIBUTION AND HOSTS

The distribution of *Carcinonemertes carcinophila carcinophila* (Kölliker) in respect to both geographical localities and hosts is indicated in Table 3.

#### *CARCINONEMERTES CARCINOPHILA* (KÖLLIKER) VAR. *IMMINUTA* VAR. NOV.

SPECIMENS OF *Carcinonemertes carcinophila* (Kölliker) were found at Grand Isle, Louisiana, and collected from crabs from various parts of the West Indies and South America, which, although they conform in most respects to the *C. carcinophila carcinophila* found in New England and Europe, nevertheless show a few morphological differences. A detailed description of these worms, constituting a new variety, *Carcinonemertes carcinophila* var. *imminuta*, taken from *Callinectes sapidus* Rathbun, at Grand Isle, Louisiana, is given below.

#### MORPHOLOGY

*Shape and Size.*—Sexually mature individuals, which are found only on the egg masses of the crab, are greatly elongated, filiform, cylindrical worms, tapered bluntly at both ends. Each worm secretes around itself a closely fitting, lapilliform sheath of semi-transparent material. Within

TABLE 4.—SIZES (IN MM) OF MATURE FEMALE *C. carcinophila* VAR. *imminuta*

Length (extended)	Width	Number of Ovaries
0.420	0.098	8 on left, 7 on right
1.480	0.162	12 on each side
1.665	0.177	9 on left, 10 on right
7.0	0.210	44 on each side
15.0	0.220	67 on each side
20.0	0.220	130 on each side
23.0	0.240	120 on each side
25.0	0.230	145 on each side
26.0	0.240	147 on each side
27.0	0.270	100 on each side
35.0	0.300	185 on each side

the sheath the worm can move about, forward or backward, or even double upon itself. The largest mature individuals usually attach their sheaths near the bases of the endopodites and consequently are well hidden among the eggs of the crab. Younger individuals are often abundant on the periphery of the egg mass.

Sexually mature females reach greater lengths than do the males. The largest adult female seen measured 35.0 by 0.3 mm when extended and 15.0 by 0.35 mm when contracted. The smallest adult female was 0.420 by 0.098 mm, when measured under slight pressure of a cover-glass. A number of adult females were measured to obtain some idea of the average size. Their measurements are shown in Table 4. The average length of these eleven worms is 16.55 mm and the average width 0.22 mm. The averages are not exact, however, because precise measurement of the very sensitive and highly contractile bodies often makes measurement practically impossible. In general, from the writer's numerous observations on living specimens, it may be said that adult females from 10 to 30 mm in length are found much more often than individuals of other sizes. In passing, it may be noted that the number of ovaries increases with the length of the worm, an observation to which reference will be made later.

Sexually ripe males tend to be smaller, and never reach the maximum size of the females. Although the same difficulties encountered in measuring the females were present here also, the figures shown in Table 5 were recorded. These twelve males show an average length of 8.68 mm and an average width of 0.214 mm. The largest adult male observed was 16.0 by 0.27 mm and the smallest, 0.928 by 0.131 mm. The sizes most often encountered were between 5 and 15 mm in length. The testes are not arranged with regularity as are the ovaries, but are scattered in the body. Hence their number was not counted, although it is probable almost beyond any doubt that they increase in number similarly with the lengthening of the worm.

A real sexual difference in size exists in this and other species of the

TABLE 5.—SIZES (IN MM) OF MATURE MALE *C. carcinophila* VAR. *imminuta*

Length (extended)	Width	Length (extended)	Width
0.928	0.131	10.0	0.23
1.036	0.144	11.0	0.24
1.202	0.181	11.0	0.23
9.0	0.21	12.0	0.25
10.0	0.26	12.0	0.22
10.0	0.20	16.0	0.27

genus *Carcinonemertes*. Bürger (1904, p. 25) gave the following measurements for *C. carcinophila*: length of female 40 to 50 mm, length of male 30 mm. The same author (1897-1907, p. 420) gave for the males 30 mm and for the females 40 to 70 mm. The measurements given in the preceding paragraphs of *C. c. imminuta* show the mature females to be often two to three times as long as the males. It is true, of course, that individual females can be selected which will be much shorter than the largest males. On the other hand, the fact remains that males have never been observed to reach as great lengths as the females. Van Beneden (1861, p. 20) stated that in *Polia involuta* (= *Carcinonemertes carcinophila*), from *Carcinides* (= *Carcinus*) *maenas* (Linnaeus) in Belgium, the females are 2 to 3 cm long, while the males are only 1 cm in length. Takakura (1910) stated that in the Japanese species *C. mitsukurii* Takakura the females are 3 cm or more in length, while the males are only 1 cm long. The situation in the Californian species *C. epialti* Coe may be similarly dimorphic, although according to Coe (1902a) the sexually mature individuals measure from 4 to 6 mm in length. However, *C. epialti* is a small-sized species and differences in size between the sexes would consequently be more difficult to recognize. Perhaps future work will disclose such differences. Coe (1920) stated that in the nemerteans "little evidence is available as to the size factor in relation to sex, but in general the exceptionally large individuals are females."

There are no indications of any suckers, hooks, adhesive pads, or clasping organs, structures which are often found in parasitic animals. The body is smooth and of the same diameter throughout (fig. 42).

The small size at which sexual maturity is reached in some individuals is remarkable, in that no other nemerteans are known to the writer to become sexually mature at such minute sizes. Bürger (1897-1907, p. 35) stated that among the Nemertea "Die kleinsten sind 3-10 mm lang und nur den Bruchtheil eines Millimeters breit (Oerstedia)." Böhmig (1933, p. 4) gave as the lower limit of length 5-10 mm. Coe (1905a, p. 5) mentioned minute species of *Tetrastemma* but 5 mm long and 0.5 mm thick when sexually mature. Willemoes-Suhm (1874, p. 411) in a brief description of the nemertean which he found on the abdomen of *Planes* (= *Nautilograpsus*) *minutus* (Linnaeus) stated that the worm did not exceed 2 mm. However, none of the specimens examined by him had the genital organs developed. Van Beneden (1861, p. 18) stated that in *Polia involuta* (= *Carcinonemertes carcinophila*) "On trouve déjà dans leur gaine, entre les oeufs de crabe, des jeunes qui n'ont pas plus du double de leur largeur." Whether these were sexually mature individuals was not definitely stated. Friedrich (1933) found specimens of *Arenonemertes microps* Friedrich which were only 2-3 mm in length



when mature. *Carcinonemertes carcinophila* var. *imminuta* reaches sexual maturity at the smallest sizes known for any nemertean.

*Body Surface*.—The entire body is ciliated (figs. 14-19). At the anterior end there is a minute funnel-like depression about  $20\ \mu$  in diameter, which is the opening of the rhynchodaeum. Through this opening in the body wall the food enters the body. The sphincter-like walls around the opening are capable of great extension. In most live worms, this opening is difficult to see under ordinary powers of magnification because of the opaque, refractile quality of the surrounding parenchyma and gland cells. The anus (fig. 15, A) is situated at the posterior end of the body. This posterior opening is about the same size as that of the rhynchodaeum, and the surrounding walls are capable of extension to allow material from the alimentary canal to pass out of the body. There are no other landmarks on the body surface than the entrance to and the exit from the alimentary canal. Such organs as cephalic slits and furrows, sensory pits, and frontal sense organs are absent.

*Color*.—Many adjectives have been used by various authors to describe the color of *C. carcinophila*. The color of the variety *imminuta* appears to be no different from that of *carcinophila*. Coe (1902a) described the color of the latter as "yellowish, orange, pale reddish, rose-pink (McIntosh), or bright brick-red." Immature specimens of *C. c. imminuta* and those in which the gonads are not well developed are rather uniformly orange-red to flesh color. This color makes their detection on newly laid crab eggs, which are bright orange-yellow, rather difficult. As the crab eggs become older, their color darkens to a rich brown or black, and on these eggs the worms are readily visible. When an individual worm is placed on a glass slide, it appears whitish, especially if flattened under a coverglass. However, if several worms are allowed to crawl together in a finger bowl, the color of the resulting mass is a bright orange-red.

A delicate distinction in color exists in the two sexes when mature. The males are whiter and lack much of the orange-red shade. The difference in color is probably accounted for by the absence of large intestinal diverticula and by the appearance of abundant light yellowish or opaque testes. Under low power the alimentary canal appears as a straight, broad, grayish line, about one-third the diameter of the worm. Large mature females are flesh-colored to orange-red, sometimes even approaching a bright red. The large intestinal diverticula with their yellow to orange-brown walls and the abundance of eggs are probably factors in increasing the intensity of color in the female. Individuals which are flattened out under a coverslip appear similar in color in transmitted light. However, with practice, it is relatively easy to distinguish

sexes when the worms are still on the egg masses. The larger the mature worms the more pronounced the color differences seem to be. The cephalic region generally appears somewhat paler than the rest of the body because of the nearly colorless esophagus and proboscis and the absence of the gonads and intestine in that region.

Differences in color between the sexes are already well known in the Nemertea, although they have been previously unrecognized in Carcinonemertes. Riepen (1933, p. 332) described the color of *Malacobdella grossa* (Müller) as follows:

Die Männchen sind zumeist weisslich bis grau, die Weibchen gelblich bis bräunlich gefärbt. Dadurch ist ein sicheres äusseres Unterscheidungsmerkmal der Geschlechter werden. Bei geschlechtsreifen Weibchen tritt der Unterscheid vom Männchen ausserdem dadurch hervor, dass die seitlichen Partien der hinteren Körperhälfte gegenüber dem übrigen Körper bedeutend dunkler (tief braun) gefärbt sind. Diese Erscheinung ist auf den Inhalt der Ovarialsäckchen (Eier und deren mit Dottermaterialien angefüllten Nährzellen, siehe Kapitel Gonaden) zurückzuführen. Die von Spermatozoenmassen erfüllten Hodensäckchen sind von milchigweisser Farbe, so dass bei den Männchen die Gonadenregion vom übrigen Körper nicht merklich abgehoben erscheint.

In *Cerebratulus lacteus* (Leidy) and in many other species there is, as mentioned by Coe (1920), sexual dimorphism in respect to color, although this differentiation may be apparent only seasonally during the reproductive period. Coe stated that "it seems not improbable that the sexes in every species if carefully observed would likewise be recognizable by color modifications when their sexual products are ripe."

*Ocelli*.—There are two dark yellowish-brown ocelli located laterally just anterior to the brain. In one mature female the two ocelli were located 80  $\mu$  in front of the brain, 200  $\mu$  from the anterior end of the body, 135  $\mu$  apart, and 35  $\mu$  from the sides of the body. Under low power they appear dark brown or black and more or less irregularly shaped (figs. 20, 50, and 52). Under high dry magnification the ocelli are observed to be composed of groups of light brown granules 0.4  $\mu$  in diameter. These granules are most thickly congregated in the center of the ocellus, imparting a very dark brown, almost black, color to that region. The peripheral area of the ocellus, where the granules are more scattered, is light yellowish-brown. The ocelli are 20 to 70  $\mu$  in diameter. Often the shape is not at all regular. Sometimes the yellow-brown granules are scattered at random over parts of the head region. The ocelli may not be of the same size or shape on the two sides of a single individual. One worm taken from the gills of a crab had only a right ocellus. Another worm, a mature female from an egg mass, had two pairs of ocelli, making four in all. A second pair was located at the level of the posterior margins of the brain lobes. These were only about one-sixth as large as the anterior pair. Another worm had two extra ocelli located close together at the anterior edge of the dorsal commissure of the

brain. Coe (1902b) mentioned that the two ocelli in this genus are occasionally fragmented into four. The position of the ocelli in the body will be mentioned below in the discussion of the nervous system.

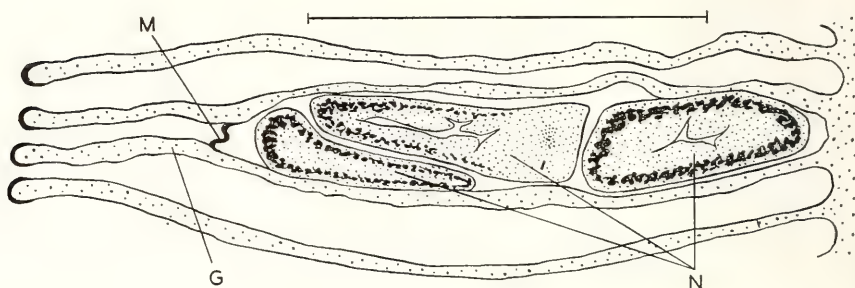
*Movements.*—The worms are incapable of any swimming movements and depend upon a substratum for locomotion. The thousands of cilia on the outside of the body beat in successive waves and carry the worm forward. A large amount of mucus is secreted by the dermal and sub-muscular glands, which aids the worm in adhering to the substratum. As the worm proceeds a glistening trail of mucus is left behind. The anterior end of the body is almost constantly performing exploring motions while the worm is moving. That part of the body is very sensitive to mechanical stimuli. The movement of the worm is a gliding motion, resembling that of *Planaria* and other *Turbellaria*. There are no strong peristaltic waves of contraction and no undulatory movements, such as are present in many nemerteans. The production of mucus is no doubt of great advantage to the worms, since it enables them to adhere to the carapace of the crab or to the endopodite hairs or eggs, withstanding the currents of water which might otherwise throw them off. The mucus also provides a suitably soft, yet resistant, substratum against which the cilia can work (Friedrich, 1932, p. 539).

When the worms are violently stimulated, by pinching, lack of water, acids and other strong chemicals, etc., they may contract the musculature of the body wall, throwing themselves into variously coiled masses. Strong peristaltic movements may occur under such stimulation. In the normal, unstimulated worm, gentle waves of contractions pass along the body, aiding indirectly the movement of food materials in the alimentary canal.

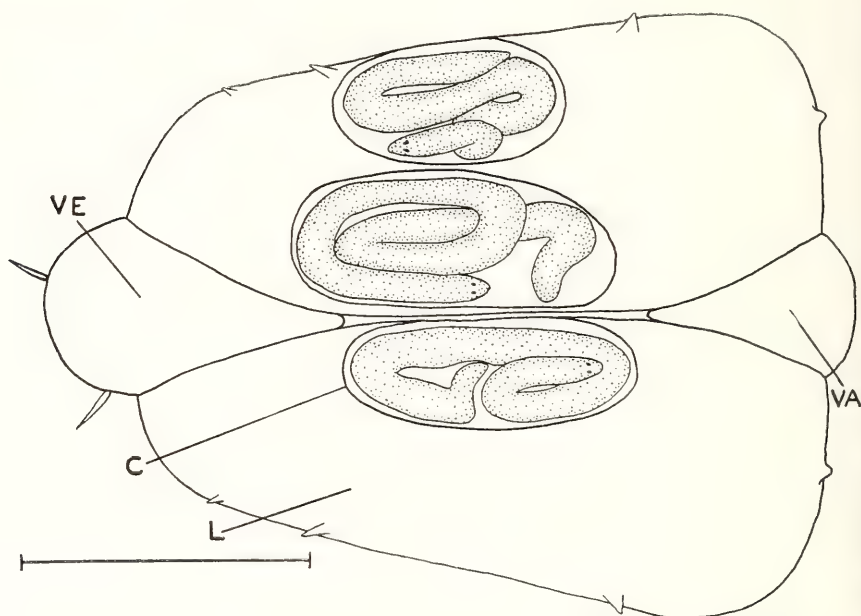
Adult worms of both sexes are negatively phototactic. When infested egg masses are placed in a finger bowl of clean sea water, many of the worms leave their mucous sheaths and crawl to the side of the dish away from the source of light. Worms on the gills of the crab seem to be even more strongly negative in their reaction to light. When infested gills are placed in a finger bowl of sea water, within a few minutes the worms break through their delicate capsule walls (text fig. 1, M) and crawl quickly to the darkest part of the dish. There they pile up on one another in an orange-red mass. When the dish is then turned 180 degrees a mass streaming of the worms across the bottom of the dish back to the opposite side away from the source of light occurs. Such negative phototaxis is not rare in the Nemertea. In fact, according to Böhmig (1933, p. 60), all adult nemerteans behave thus, except perhaps *Oerstedia dorsalis* (Abildgaard), which according to the observations of von Buddenbrock (1923, p. 1) is positively phototactic. The free-swimming young forms of *C. c. imminuta* are positively phototactic, a phenomenon which will be



mentioned below in the discussion of the life history. When heavily infested egg masses are placed in a finger bowl of clean sea water, the water on the side nearest the source of light becomes cloudy with free-swimming larvae within a few hours. The smallest crawling worms observed were weakly negative to light, but those from about one



TEXT FIG. 1.—Longitudinal section of infested gill of *Callinectes sapidus*, showing capsule and coiled nemertean. Stained with Delafield's haematoxylin and eosin. Scale 1 mm. M, mucous wall of capsule secreted by nemertean; G, gill lamella; N, body of nemertean.



TEXT FIG. 2.—End view of gill lamella of *Callinectes sapidus* showing position of worm capsules. Scale 2 mm. VA, afferent blood vessel; C, capsule of nemertean; L, lamella of gill; VE, efferent blood vessel.

millimeter in length showed definite negative phototaxis. There is, then, a reversal in response to light occurring probably at the time when the free-swimming larva settles down to a crawling existence. Such a reversal of response has been observed by Reisinger (1926, p. 9) in the fresh-water nemertean *Prostoma graecense* Böhmig.

*Location on Host Crab.*—Sexually mature worms were found only on the egg masses of the crabs, although worms in which rudiments of ovaries could be distinguished were found occasionally on the gills. In one of these there were eight pairs of ovaries, each about  $40\ \mu$  in diameter and composed of several large, granular, whitish cells. Each rudimentary ovary was situated in a slight invagination of the intestinal wall. Most of the worms on the gills, however, show no indication of gonads when observed under low power *in vivo*. All the worms on the gills live irregularly coiled in capsules between the gill lamellae (text fig. 2). A wall of what is apparently hardened mucus (text fig. 1, M) secreted by the worm cements the two lamellae together, closing off free communication between the worm in its capsule and the surrounding sea water. Only one worm occupies each capsule. As many as six such capsules have been observed between two gill lamellae. Heavily infested gills may harbor several hundred worms.

Sexually ripe males and females, as well as those nearly mature and those which have recently spent their sex products, are found scattered on the egg masses of the crab. The adults most often occur concealed among the eggs, however. The mucous sheaths in which they live are usually attached near the bases of the endopodites. Occasionally mature worms of small size are found on the periphery of the egg mass, but here immature worms or worms in which the gonads are just beginning to form are more common.

*Mucous Sheaths.*—The mucous sheaths, in which the adult worms live, are apparently of the same structure in the two sexes. The proximal end of the case is fastened to the endopodite hair of the crab. The exact point of attachment is indistinguishable. The mucous material of the sheath is continuous with the material which covers the endopodite hairs. The middle region and distal end of the case are unattached. One of the largest sheaths seen, that of an adult female, measured 25 mm in length. The sheaths are elastic and can be stretched to two or three times their original lengths. The surface of the sheath is lapilliiform, that is, covered more or less completely with small, irregularly shaped, raised concretions (figs. 7, 12, 13, and 32). These are largest in the middle region of the sheath (fig. 13) and decrease in size toward both ends, finally disappearing entirely (figs. 7 and 12). As they diminish in size they tend to be more angular and become more numerous. There is no regular pattern in their arrangement and even in the middle region of the sheath, where

most of the concretions are large, a few smaller ones may be found among them. When viewed under high power the raised areas show concentric striae resembling growth lines. The walls of the sheaths are thin and transparent, and, except in the central lapilliform region, are collapsible. When the worm withdraws, the walls wrinkle and come together. Possibly the concretions of the mucus-like substance of the middle region serve to prevent the collapse of the sheath and thus to offset the consequent pressure on the body of the worm.

Although the sheaths vary in length, they are always longer than the worm in its contracted state. The sheath of a very small adult female, 1.665 by 0.177 mm, (fig. 32) showed none of the prominent raised lapilli, but faint markings on the surface may indicate their future positions. The promixal part of the sheath showed coarse, irregular granulations. There were several longitudinal folds in the central region, probably caused by the collapse of the walls, when the worm retreated from the sheath.

At the time of egg laying, part of the sheath becomes a container of the eggs (fig. 21). As will be mentioned again, the female deposits eggs which adhere all about her to the wall of the sheath. She then retreats from the scene, the elastic walls of the sheath contract and the result is a tube filled with eggs. The female sometimes forms one or several branches to the main sheath, in which she deposits her eggs. She may, however, simply lay her eggs in an extension of her own sheath. The wall of that part of the sheath which encloses the eggs never bears the lapilli found on the main section of the sheath, probably because the temporary nature of the egg sheath does not allow time for the formation of such lapilli. The sheaths of male worms occasionally show side-branches, although certainly these are not used for egg-laying. The egg sheaths sometimes contain enormous numbers of eggs. One such sheath 10 mm in length was estimated to hold 1200 eggs.

Sexually mature worms of both sexes, as well as those showing no evidence of gonads *in vivo* and those which had already given off their sex products, were found living in sheaths. In fact, no sexually mature worms were seen outside the sheaths, except hours after the capture of the crab, when the worms had been irritated by abnormal stimuli. Only one worm was seen in a sheath at one time. Van Beneden (1861, p. 20) stated that in *Polia involuta* (= *C. carcinophila*) he often found "des individus des deux sexes logés dans la même gaine." It seems beyond doubt to the writer that the two sexes must at times be together in the same sheath to bring about insemination. Otherwise the spermatozoa, which are limited in number as compared with the huge numbers present in some of the larger free-living nemerteans, would be so scattered that the majority of them would never come in contact with a female worm.



Probably the mucous sheath aids in bringing about the entrance of the spermatozoa into the ovarian ducts by confining the former until they make contact with the female. In passing, it should be mentioned that among the preserved specimens of the new species from Zanzibar to be described below there was one mucous sheath which contained both a male and a female worm.

When sectioned and stained with haematoxylin the lapilli on the sheaths stain more lightly than the thin wall of the sheath upon which they are situated (fig. 6). A cross section of a lapillus shows distinct longitudinal striae (fig. 6) in the inner half, while the outer half is opaque and granular. The outer half furthermore is stained only lightly, while the inner half becomes a light purplish blue, in contrast to the dark purplish blue color assumed by the sheath wall. The largest lapilli are about  $30\ \mu$  thick. The walls of the sheath, however, measure only about  $5\ \mu$  in thickness.

*Body Wall.*—The entire body is covered with a single layer of glandular and ciliated cells (figs. 14 to 19). In four living worms the height of these cells was 10, 9, 11, and  $13\ \mu$  respectively, averaging about  $10\text{--}11\ \mu$ . On the anterior end of the body the layer is thicker, measuring  $22\ \mu$  in height. In fixed and stained material the epithelium measures  $10\ \mu$  in thickness. Each ciliated cell contains distally a group of 8 to 12 minute granules which stain deeply with neutral red (10 drops of dilute neutral red solution in a finger bowl of sea water left overnight). In the middle region of the cell there is a slightly elliptical nucleus lying parallel to the long axis of the cell. When viewed in any one optical plane approximately six cilia can be seen along the distal margin of the cell. These average  $4.5\ \mu$  in length over most of the body, but are  $6\ \mu$  long on the anterior end. The ciliated cells on the anterior end of the body are not only taller but also relatively more slender than the cells covering the rest of the body. Gland cells are fewer in number. In a worm whose epithelium has been stained with neutral red the large gland cells filled with a reddish stained secretion can be seen clearly under oil immersion. They are more numerous in the head region and hence that region stains more deeply with neutral red.

Immediately below the outer layer of cells there is a thin basement membrane  $0.5\ \mu$  thick. Because of its extreme thinness and hyaline nature this structure is hardly distinguishable in life even under high magnification. In sectioned material stained with fast green or with Delafield's haematoxylin the membrane is colored strongly, appearing as a fine line extending around the body just below the epithelial cells of the integument.

Internal to the basement membrane there is an extremely thin layer of circular muscles. The entire layer is not over  $1.5\ \mu$  thick in sectioned

worms. In living animals the fibers are extremely difficult to make out in any detail. Each fiber seen in fixed and stained material is about  $1\ \mu$  or less in diameter. In longitudinal sections the fibers can be seen as faintly stained lines superimposed upon the relatively massive longitudinal fibers. The weak development of the circular muscle fibers probably accounts both for the absence of strong peristalsis and for the inability of these worms to fragment the body. At the opening of the rhynchodaeum and at the anus the circular fibers no doubt act as sphincter muscles (fig. 15, CM).

A layer of longitudinal fibers is situated immediately below the circular layer. Like the latter this layer forms a continuous muscle tube around the body. In life the individual fibers are not distinctly visible, but in sectioned and stained specimens they show prominently, especially when Delafield's or Heidenhain's haematoxylin is used. The longitudinal layer as seen in the extended living worm is usually 2 to 3 times ( $3\text{--}5\ \mu$ ) as thick as the circular layer. The relative thickness of the two layers varies greatly with the state of contraction of the body. In some sectioned specimens, which were highly contracted when fixed, the longitudinal layer is as much as 10 to 15 times ( $15\text{--}22\ \mu$ ) as thick as the circular layer (figs. 17 and 19, LM). In life the longitudinal layer is marked with fine longitudinal, refractile lines—the edges of the individual muscle fibers. The fibers seen in sections show no nuclei and no cross striations, and their substance appears to be homogeneous. Each fiber is greatly elongated, measuring  $1.5\ \mu$  in diameter and reaching sometimes more than  $100\ \mu$  in length. Nuclei if present must be very minute. Coe (1905a, p. 14), while discussing the musculature of the Nemertea, stated that "Each muscle fiber consists of a single cell, with an extremely small, slender nucleus, surrounded by an insignificant amount of undifferentiated cytoplasm. This minute cell body lies upon, or imbedded in, the fiber of contractile substance." Between the loosely arranged fibers the necks of the submuscular glands extend outward to the integumental epithelium.

Anteriorly to the level of the brain the longitudinal muscle layer decreases in thickness. The fibers bend inward, passing among the cephalic glands and parenchymal cells (cf. fig. 9). Many of the fibers extend transversely, others obliquely. Along the rhynchodaeum, where the majority of these fibers are located (fig. 16), there are longitudinal fibers also. In living worms under high magnification, twitches in the region surrounding the rhynchodaeum and changes in the diameter of the latter are often seen. Such movements are accomplished by the contraction and relaxation of the cephalic muscle fibers. When the esophagus is everted, as will be described later, these fibers no doubt aid in increasing the diameter of the rhynchodaeum. They may also aid in forcing out

the contents of the cephalic glands. A few scattered fibers may be seen in sections of the area around the brain, the anterior part of the esophagus, and the proboscis, although none of the fibers are connected to the latter. These are probably the fibers described by McIntosh (1873-1874, Pl. XIV, fig. 4, f) as "powerful transverse fibres which retain the posterior part of the oesophagus *in situ*." Regarding the cephalic muscles of nemerteans, Coe (1905a, p. 12) stated: "In the cephalic region of the Heteronemertea and many of the Palaeonemertea, the arrangement of the muscular layers is broken up to form a complex network of fibers running in all possible directions, but of which the longitudinal fibers are the most numerous. In other forms the two muscular layers extend forward into the head." Cephalic muscle fibers have not been previously described in *Carcinonemertes*.

Anterior to the brain the head is almost completely filled with clusters of cephalic glands (fig. 16, CG), which open to the outside by numerous ducts over the surface of the head. The cephalic muscle fibers pass through the masses of gland cells, and possibly aid in expelling the secretions of the glands by their contractions. Laterally to the brain lobes the cephalic glands merge gradually with the submuscular glands. In haematoxylin or safranin stained sections the cephalic glands do not become colored as deeply as the submuscular glands, and consequently they are sometimes more difficult to identify. The cell outlines are not as distinct as those of the submuscular glands. However, in sections fixed in Schaudinn's fluid and stained with methylene blue and eosin, the gland cells of both cephalic and submuscular regions become stained bright blue against a pink background.

Immediately beneath the longitudinal muscle layer there is situated a massively developed layer of gland cells, the submuscular or hypodermal glands. The contents of these glands stain heavily with safranin and with Delafield's haematoxylin. For this reason they are conspicuous in sections even under low power magnification. The layer is as thick as or thicker than the outer layers of the body wall combined. Measuring from the exterior of the body to the inner ends of the gland cells gives a distance of 50 to 70  $\mu$ . The gland cells are not simple, but several are grouped together, with their ducts converging in a common duct to the exterior. Commonly four or five such cells empty by a common duct. The ducts pass among the muscle fibers, through the basement membrane, and among the cells of the integumental epithelium, to discharge their glandular secretion to the outside of the body. The gland cell nuclei (fig. 40, S), about 1  $\mu$  in diameter, are located in the proximal half of the cells, below the muscle layers. In life the contents of the gland cells stain red with neutral red and are coarsely granular and refractile. In fixed,



sectioned, and stained material the secretion appears finely granular and deeply stained.

Most nemerteans do not have such a remarkable development of the submuscular glands. According to Coe (1905a, p. 18) these glands are usually found only in the head region or occasionally in the region of the esophagus, as in *Amphiporus nebulosus* Coe, or reaching to the anterior end of the intestine, as in *Emplectonema bürgeri* Coe. Bürger (1897-1907, p. 67) stated that "Nur bei den Eupolien werden sie im Allgemeinen recht ansehnlich an Länge und Umfang. Hier erstrecken sie sich in die Vorderdarmregion hinein." The great extent and size of the submuscular gland layer was given by Coe (1902b) as a generic character of *Carcinonemertes*.

*Connective Tissue and Parenchyma.*—Delicate strands of connective tissue can occasionally be seen in sections among the necks of the submuscular glands, immediately internal to the longitudinal muscle layer, and among the muscle fibers. The parenchyma is greatly reduced. The intestine fills practically all the space internal to the submuscular glands (fig. 19). A few minute nuclei are scattered along the edge of the intestine, and from these the gonads probably eventually develop. Such a process has been described by Coe (1905a, pp. 64-65) for nemerteans in general. In the cephalic region anterior to the brain the parenchyma is most abundant. It fills all the space between the rhynchodaeum and the muscle layers of the body wall which is not occupied by the rhynchodaeum, muscle fibers, gland cells, nerves, or ocelli. The scarcity of parenchymal tissues in *C. carcinophila imminuta* makes a decided contrast with species like *Amphiporus gelatinosus* Coe, in which the parenchyma is several times thicker than the body wall.

*Alimentary Canal.*—The rhynchodaeum (fig. 16, RH) is a straight, slender tube, extending from the opening on the anterior end of the body to the region close in front of the brain, where it gives off ventrally the esophagus and dorsally the proboscis. Its lumen is about  $7\ \mu$  in diameter and its wall  $3.5\ \mu$  in thickness, making a total diameter of about  $14\ \mu$ . It is embedded in the parenchyma of the head and surrounded by the very loose network of longitudinal, transverse, and oblique cephalic muscle fibers. The non-glandular wall of the rhynchodaeum is composed of a single layer of small, columnar, ciliated cells.

The esophagus (fig. 16, AE and PE) leaves the ventral wall of the rhynchodaeum a short distance anterior to the brain in the mid-line of the body. The anterior part, extending from the rhynchodaeum under the ventral nerve commissure to a region just posterior to the rear margin of the brain, has about the same diameter as the rhynchodaeum. As it passes posteriorly it increases gradually in diameter to about  $80\ \mu$ , and its walls become folded longitudinally. In life this part of the esophagus

(fig. 16, AE) is opaque and granular, with longitudinal refractile lines caused by the folding of the wall. Both ciliated and glandular cells are to be found in its wall. The posterior end of this section of the esophagus fits like a cap on the anterior end of the thick-walled, muscular posterior part (fig. 16, PE). The junction between the two histologically very different parts is well demarcated, and located usually at about the level of the stylet (fig. 16). In a relaxed, actively crawling worm the posterior part of the esophagus lies entirely posterior to the brain. Its general shape is dolioform, with the anterior end squarely truncate where it joins the slender anterior part, and with the posterior end tapering somewhat abruptly before joining the intestine. The posterior sections of the esophagi of ten adult worms measured 85 by 50, 90 by 65, 127 by 117, 147 by 120, 150 by 80, 162 by 95, 190 by 85, 200 by 147, 252 by 140, and 378 by 41  $\mu$  respectively. The esophagus is always longer than its diameter. The ten measurements gave an average length of 178  $\mu$  and an average diameter of 97  $\mu$ .

The posterior part of the esophagus in the live worm is very conspicuous both by its whitish color and by the anterior and posterior contractions of its body wall. The ciliated and glandular epithelial lining is surrounded externally by a layer of distinct circular muscle fibers, which in their shape, size, and staining resemble those of the body wall and head. Occasionally a few longitudinal muscle fibers may be seen external to the circular layer. These are more weakly developed however. The entire wall measures 17  $\mu$  in thickness, leaving a spacious lumen of about 150  $\mu$  in diameter.

In contracted worms under pressure of the coverglass the esophagus may be moved forward so that it lies almost wholly anterior to the brain (figs. 50 and 52). In three worms the esophagus was observed to move anteriorly until the thin anterior part was everted outside the body (fig. 52, AE) and the muscular posterior part (fig. 52, PE), its circular muscles contracting spasmodically, reached nearly to the inner edge of the integumental epithelium. Partial eversion of the esophagus was sometimes seen in worms placed in sea water on a slide with no coverglass. In two worms under pressure the anterior part was completely everted, so that the posterior part was brought completely outside the body. The latter continually underwent convulsive peristaltic contractions of the circular muscle fibers, beginning at the anterior end and progressing rapidly posteriorly. In both cases the worms kept the esophagus everted for only a few seconds, so that a camera lucida drawing was impossible. However, sketches of one of the worms were made (fig. 51, A, B, and C). The arrow shows the direction of peristaltic contractions. Both worms were able to withdraw their esophagi and apparently were uninjured by the experience. When the esophagus is thus everted the proboscis is at the

same time drawn far anterior to its normal position behind the brain. However, the esophagus is responsible for the movement of the proboscis. The latter is entirely passive, showing no contractions of any of its parts which might alter its position in the body.

Van Beneden (1861, Pl. III, fig. 5) published a drawing of the anterior end of the head of *Polia involuta* (= *C. carcinophila*) in which the esophagus, and not the "proboscis" as Van Beneden interpreted it, is everted. The thick walls and the ciliated interior of the everted part both indicate that it is the posterior muscular part of the esophagus and not the proboscis which is everted. At the distal end of the everted structure Van Beneden represented three curved, spine-like objects, unmentioned in the text of his paper. These may have been bunches of cilia. Certainly they are not stylets, since this species has only one. The writer suspects that this figure was drawn very hastily, since the worms do not keep their esophagi everted for more than a few seconds, and then perhaps copied later from sketches or from memory.

The posterior end of the esophagus is surrounded by the anterior end of the intestine, into which it empties directly. The intestine extends in the middle region of the body posteriorly to the anus. As already mentioned, the yellow-orange to brown color of the intestinal walls contributes greatly to the general color of the worm. In sexually mature females the intestine is deeply lobed on both sides of the body (fig. 34), probably because of the pressure of the alternating ovaries. In young worms or those in which the ovaries are undeveloped, there is only a very slight and somewhat irregular crenation of the intestinal wall. In adult males the wall is likewise nearly straight, since the irregular disposition of the numerous testes does not create local pressures on the intestine to force the wall into pouches. The walls of the intestine are, however, slightly scalloped to fit the contours of the contiguous testes. The shape of the intestinal pouches varies with the size of the ovaries and the state of contraction of the worm. When the worm is contracted the pouches are located usually directly opposite one another, but when extended the pouches alternate in a zigzag course. The number of pouches varies with the size and age of the individual (Table 4). The smallest number of pouches observed was 15 (8 on the left and 7 on the right) in an adult female 0.420 by 0.098 mm. The largest number found was 370 (185 on each side) in an adult female 35.0 by 0.3 mm. The anterior end of the intestine in large females usually lacks pouches for a distance of about 1 mm, the ovaries being absent there. The first few anterior pouches are small, but increase in size as the ovaries increase. Thereafter, both pouches and ovaries are approximately the same size until the posterior part of the body is reached. There the last few pouches diminish in size



with the dwindling ovaries, and, when the intestine passes posteriorly to the blood vessel and nerve commissures, its border is straight.

The intestine contains a great number of clear globules (fig. 47)  $4\text{--}12\ \mu$  in diameter, which are suspended in a fluid substance. In addition there are often numerous dark brown or black particles of irregular or oval shapes. These measure from very small sizes up to  $25\ \mu$  in length. Some of the chromatophores in the crab embryos are of similar size and shape. The fact that these particles were found only in worms removed from brown egg masses, in which the crab embryos are well pigmented, and never in worms taken from the gills, together with the additional evidence that they were absent in worms from yellow-orange egg masses, in which the crab embryos are as yet unpigmented, leads the writer to the conclusion that these nemerteans are able to feed upon the crab eggs. The mechanism of this is unknown since the process has never been observed in the laboratory. It is possible that the sucking action of the powerful muscular esophagus can break the egg membrane by continued pulling and then draw out the soft embryo within. Parts of crab embryos were seen in the intestine of a nemertean from *Callinectes marginatus* (Milne-Edwards), to be described below. The walls of the intestine have no contractility of their own and contain no muscle fibers. However, when the body wall contracts, the contents of the intestine are moved violently back and forth.

The intestinal wall (figs. 14, 15, 16, 18, 19, and 40, I) consists of a single layer of tall, columnar cells which probably are sparsely ciliated, although this detail could not be ascertained from the material available to the writer. Coe (1905a, p. 22) stated that in the nemerteans "these cells are actually provided each with a few very long cilia of such delicacy that they are seldom distinguishable in prepared sections, although they are readily demonstrated in life." Each cell contains a nucleus in its central region and numerous small granules which stain deeply with safranin or Delafield's haematoxylin scattered through the cytoplasm.

The intestine opens at the posterior end of the body (figs. 15 and 20, A) at the base of a terminal, funnel-like depression. The anus has no definite limits, but is a simple tube about  $5\ \mu$  in diameter in sectioned material, capable of some distension in life, which passes through the layers of the body wall to allow the discharge of materials from the intestine. In the region of the anus the musculature of the body wall disappears and the integumental epithelium becomes continuous with the intestinal epithelium. The circular muscle layer of the body wall forms a sphincter muscle around the anus, controlling its opening and closing (fig. 15, CM).

*Proboscis*.—The proboscis, situated dorsally and somewhat laterally

to the esophagus (figs. 16 and 20, AC, MC, and PC), is very much reduced in size, reaching posteriorly scarcely beyond the posterior end of the esophagus. It is divided into three chambers, anterior, middle, and posterior, the cavities of which are continuous. The anterior chamber (fig. 16, AC) extends only to the level of the posterior limits of the brain, in decided contrast to most Hoplonemertea in which the anterior chamber constitutes by far the major part of the proboscis and the stylet apparatus is located far posteriorly in the body. In *C. c. imminuta* the stylet apparatus (fig. 16, BA) is located at the level of the muscular part of the esophagus. The round middle chamber (fig. 16, MC) and the elongated posterior chamber (fig. 16, PC) follow. The length of the proboscis varies in different specimens, but it usually extends to the anterior end of the intestine, a distance of approximately 0.42 mm from its point of origin in the dorsal wall of the rhynchodaeum. The shape of the proboscis depends on the state of contraction of the worm. In a relaxed worm the proboscis may be ten times longer than its diameter, but in a contracted specimen, only four times its diameter.

The proboscis sheath is very much reduced. According to Coe (1902a) the sheath of *C. epialti* Coe "consists merely of a few fibers of connective tissue, supporting a very thin, flattened epithelium, and can be seen only in favorable preparations." In *C. c. imminuta* no trace of the proboscis sheath could be seen in life, and in sections only a few delicate strands of connective tissue, probably belonging to the sheath, can be seen at the junction of the middle and posterior chambers. These strands may be only parts of parenchymal cells however. The muscles attached to the proboscis in many nemertean species are entirely absent here. The proboscis is embedded directly in the surrounding parenchyma. During the writer's observations the proboscis was never seen to move, except for very slight changes in shape of the muscular middle chamber. The whole proboscis may be pulled about in position, as described above, by the movements of the esophagus. Even when the worms were subjected to stimuli which would readily cause large, free-living species to throw out their proboscides, there was no movement of the proboscis in this species. The worms were stimulated sometimes to the point of death by heat, dilute HCl, glycerine, alcohol, fresh water, and mechanical pressure, all without eversion occurring. It is believed by Coe (1905a, p. 27) that in *Carcinonemertes* "the single stylet . . . can be everted only as far as the opening of the rhynchodaeum. . . . With the rhynchodaeum opening pressed against the tissues of the gills of the crab on which this nemertean lives the stylet can thus puncture the gills. The exuding blood and other fluids are then drawn into the nemertean's stomach where they serve as food." The worms from Grand Isle have never been seen by the writer to evert the anterior chamber of the

proboscis, which would be mechanically necessary to bring the stylet to the exterior of the body. In his description of *C. epialti*, Coe (1902a) wrote:

The stylet can hardly be moved much beyond the external opening of the rhynchodaeum, and from a study of its structure alone it is hard to conceive how it can be moved for even this short distance, imbedded as it is among the other tissues. By crushing and many kinds of stimuli I have seldom been able to cause the worms to move the stylet region to any extent either forward or backward. It nearly always remained in the vicinity of the brain. It is my opinion that the proboscis can be everted only far enough to bring the stylet a little beyond the opening of the rhynchodaeum on the tip of the snout, as figured by Van Beneden (1861), and that esophageal muscles aid in this movement. At the tip of the snout the stylet can puncture the tissues and blood vessels of the crab's gills. With the rhynchodaeum of the worm widely opened and closely applied to the point of puncture, the blood and nutritive fluids exuding from the wound can be drawn directly into the rhynchodaeum and thence into the esophagus by the contraction of the muscular walls of the latter.

Coe evidently accepted Van Beneden's drawing of what is apparently the esophagus as that of the proboscis. The writer is forced to conclude that the proboscis is incapable of eversion, and that the stylet is not used for puncturing the gills.

The anterior chamber of the proboscis (fig. 16, AC) extends from its point of origin in the dorsal wall of the rhynchodaeum immediately on front of the brain through the brain ring, formed by the ganglia with their dorsal and ventral commissures, and ends a short distance behind the brain. Its anterior end is narrow, about  $10\ \mu$  in diameter in extended worms. The posterior part gradually widens to about  $50\ \mu$ . The wall of the chamber consists of a thin flattened epithelium. No muscle fibers could be seen in the sections. The highly glandular epithelium so common in many of the Nemertea is absent. The lumen of the chamber is somewhat triangular, with the stylet apparatus protruding into it at the posterior base of the triangle.

The anterior chamber is connected with the middle chamber by a narrow canal  $35\text{--}40\ \mu$  in length, whose lumen measures  $7.5\ \mu$  in diameter. Immediately dorsal to this connecting duct there is located a thick glandular enlargement in which the basis and stylet are embedded (fig. 16, GL). The walls of the enlargement, about  $20\ \mu$  in greatest thickness and  $40\text{--}50\ \mu$  in length, surround the basis and stylet laterally but not anteriorly and posteriorly. Ventrally and dorsally to the basis the walls are very weakly developed. They are composed of a single layer of large, columnar, glandular cells, whose nuclei are situated in the distal half of the cells. In life the epithelium is opaque and yellowish, with many granules. It stains readily with neutral red, becoming a light red in color. In sections these cells stain easily with haematoxylin. These gland cells, according to Coe (1905a, pp. 36-37), empty into the anterior proboscis chamber in most Hoplonemertea. Enclosed within these glandular walls



there is an oval, clear area (figs. 16 and 36), measuring 29 by 13  $\mu$ , in which the basis and stylet are located. In life the substance in this area is hyaline with no visible structure. However, in sections treated with Heidenhain's iron haematoxylin or Feulgen's nucleal reaction, there can be seen a single layer of small cells surrounding the basis, forming as Coe (1905a, p. 36) suggested "a mold into which their secretions are poured. These secretions harden and form a basis of the exact size and shape of the mold."

The basis is cylindrical (figs. 16, 20, and 52, BA; figs. 36 and 43), though not always of exactly the same diameter throughout. Both ends are bluntly rounded. On the anterior end there is a single stylet (fig. 20, S). In life the basis is granular and refractile with a yellowish tinge. It has great affinity for orange G when stained intravitaly. In sectioned material the basis stains brilliant red with safranin, very dark purple with Delafield's haematoxylin, black with Heidenhain's iron haematoxylin, and light pinkish yellow with Feulgen's nucleal reaction.

The stylet is about  $\frac{2}{3}$  to  $\frac{1}{3}$  as long as the basis and acutely pointed anteriorly (figs. 36 and 43; fig. 20, S). In life it is hyaline, and no inner structure can be seen. In the living worm it remains unstained by orange G, Bismarck brown, Nile blue sulphate, neutral red, methyl green, or brilliant cresyl blue. Neither is it stained in sections with safranin, either of the two haematoxylin mentioned, eosin, or fast green. The writer is therefore of the opinion that the stylet consists of a non-living concretion of some kind of mineral matter, perhaps a calcium compound, since it is difficult to find in sectioned worms, most of which at some time in the process of preparation have been subjected to acids. In those sections untouched by acids, i.e., stained with safranin and fast green, the stylet is often visible. The junction of the stylet and basis is often irregularly defined and sometimes almost impossible to locate with precision. A slight constriction occurs in the stylet just anterior to its basal origin. However, measurements were made from the beginning of the hyaline stylet material, not from the constriction. The stylet is 3.5-4  $\mu$  in diameter at its base, but the length is variable. The lengths and diameters of bases and lengths of stylets of worms taken from crab gills, and hence not sexually ripe, and of mature worms of both sexes are shown in Table 6. The total average measurements for the 40 worms given above are: length of basis 21.0  $\mu$ ; diameter of basis 5.3  $\mu$ ; length of stylet 7.3  $\mu$ ; stylet: basis ratio 0.347. There are no significant differences in size of the stylet and basis between the two groups of measurements. Many of the worms found on the gills probably had been sexually mature at least once before taking up their abode on the gills, and hence they should be expected to have measurements similar to those of sexually ripe individuals from the egg masses of the crab.

When the measurements of *C. c. imminuta* in Table 6 are compared with those of *C. c. carcinophila* given in Table 1, there are seen differences in size, if not in proportions. The measurements of the two sets tend to overlap somewhat, but the sizes of the stylet and basis in *imminuta* hardly reach even the average sizes of *carcinophila*. *C. c. carcinophila* from New England ranges from 19 to 30  $\mu$  for the length of the basis, 6 to 12  $\mu$  for the stylet length, the ratio of stylet to basis being 0.316 to 0.400. *C. c. imminuta* from Grand Isle, Louisiana, ranges from 19 to 23  $\mu$  for basis length, 6 to 9.5  $\mu$  for stylet length, the S:B ratio being 0.272 to 0.461. The diameter of the basis in New England worms was given by Coe (1902a) as 6 to 8  $\mu$ . In the Louisiana worms it is only 4.5 to 6  $\mu$ .

The small, round or oval middle chamber (figs. 16 and 20, MC) lies immediately posteriorly to the glandular enlargement around the basis.

TABLE 6.—MEASUREMENTS (IN MICRONS) OF STYLET APPARATUS OF *C. c. imminuta* IN WORMS FROM GILLS (NOT SEXUALLY RIPE) AND MATURE WORMS OF BOTH SEXES

Worms from Gills				Mature Worms			
Basis		Stylet Length	Ratio S:B	Basis		Stylet Length	Ratio S:B
Length	Diameter			Length	Diameter		
19.0	...	8.5	0.447	20.0	5.5	6.5	0.325
22.0	...	8.4	0.382	20.0	5.5	6.5	0.325
21.0	...	6.5	0.309	19.0	...	7.5	0.394
19.0	...	6.0	0.316	19.5	4.5	6.5	0.333
22.0	5.0	7.0	0.318	22.0	...	7.0	0.318
22.0	5.5	7.5	0.341	23.0	5.5	7.5	0.326
22.0	5.0	6.5	0.295	21.0	5.0	7.0	0.333
20.0	4.5	6.0	0.300	23.0	5.5	8.0	0.348
21.0	4.5	6.5	0.309	23.0	...	7.5	0.326
20.0	5.5	8.0	0.400	22.0	...	6.0	0.272
22.0	5.0	6.0	0.272	22.0	6.0	6.0	0.272
20.0	5.5	7.0	0.350	19.5	5.5	9.0	0.461
22.5	5.5	9.5	0.422	20.5	5.5	7.0	0.366
22.0	5.5	6.5	0.295	21.0	5.5	8.0	0.381
20.0	5.0	8.3	0.415	20.5	5.5	6.5	0.347
22.5	5.5	7.5	0.333	21.5	5.5	7.0	0.325
20.5	5.5	7.5	0.366	19.5	5.0	6.5	0.333
22.5	5.5	7.5	0.333	20.0	5.0	8.0	0.400
21.0	5.5	8.0	0.381				
21.0	5.5	8.0	0.381				
21.5	5.5	8.5	0.395				
21.5	5.5	8.5	0.395				
21.1	5.3	7.4	0.352	20.9	5.3	7.1	0.342

Its lumen is connected with that of the anterior chamber by the above mentioned canal, and to that of the posterior chamber by a much shorter duct about  $6\ \mu$  in diameter. In some worms the chamber tapers slightly anteriorly, and its anterior wall is distinctly thinner than the posterior wall. Usually it is almost perfectly round with walls of even thickness. The diameter varies in adult worms from 20 to  $50\ \mu$ , with an average in 16 worms of  $35\ \mu$ . The wall of the chamber, between 4 and  $5\ \mu$  in thickness, is composed of a layer of longitudinal or slightly oblique muscle fibers, covered externally with a thin layer of circular fibers, and lined with a very thin flattened epithelium. In living worms the chamber is easily recognizable by its whitish color and striae (the outlines of the muscle fibers). The spacious lumen contains small, hyaline, and light brown granules suspended in a fluid material.

The third and last chamber of the proboscis is highly variable in size and shape in different individuals (figs. 16 and 20, PC). The wall of the chamber is non-muscular, and such changes as occur in its shape in the same individual are no doubt caused by contractions of the body wall and by movements of the muscular part of the esophagus, which is close by. A series of 16 adult worms of both sexes showed posterior chambers of the following sizes: smallest 34 by  $34\ \mu$ , largest 336 by  $84\ \mu$ , with an average size of 139 by  $47.5\ \mu$ . The shape varied from round (34 by  $34\ \mu$  in an adult male worm 1.2 mm in length) to greatly elongate (252 by  $19\ \mu$  or about 13 times longer than its diameter in an adult female about 15 mm long). In live worms the shape varies somewhat with the pressure of the cover glass. In relaxed worms under little pressure the chamber is usually elongate, reaching posteriorly to, or in some cases even as much as  $100\ \mu$  beyond, the anterior end of the intestine. In contracted worms under pressure the chamber occasionally is bent at an angle to the main longitudinal axis of the proboscis, although normally it lies in a line with the anterior and middle chambers.

The walls are thick and glandular, consisting of a single layer of irregular columnar cells, which contain large amounts of secretion readily stainable by haematoxylin. The thickness of the wall varies from 5 to  $16\ \mu$ . The lumen contains minute granules 3 to  $4\ \mu$  in diameter, some of which appear to stain with neutral red. The product of these glands is evidently different from the secretion of the submuscular and cephalic glands, for, while the latter types stain brilliantly with methylene blue, the secretion of the gland cells of the posterior proboscis chamber, and indeed also that of the glands associated with the basis, stains only a faint blue. Coe (1902a) thought it probable that the substance found in the middle chamber has its origin in the posterior chamber, a supposition supported by the writer's observations.



*Blood Vessels.*—There are two lateral blood vessels (fig. 20, LB; fig. 48, LV), about  $11\ \mu$  in diameter, parallel with and slightly ventral to the intestine. They lie adjacent and ventral to the nerve cords (figs. 14, 17, 18, and 19, LV). In the esophageal region the two vessels begin to converge and soon pass through the brain ring, one on either side of the proboscis. Immediately dorsal to the posterior end of the rhynchodaeum the two vessels are united in a cephalic commissure (fig. 20, AB). At the posterior end of the body the vessels are likewise joined by an anal commissure (fig. 15, BC) ventral to the intestine. In one adult worm the anal commissure was  $125\ \mu$  anterior to the hind end of the body, in a position anterior to the anal commissure of the lateral nerves. There is no trace of a dorsal vessel.

The walls of the blood vessels consist of a very thin endothelium placed upon an extremely delicate basal membrane, external to which there is a thin layer of circular muscle fibers. In living worms the vessels are capable of contractions independent of the movements of the body wall muscles. As a result of these the walls of the blood vessels are thrown into numerous bulges and bulbous projections. These can be seen well in both living and sectioned material. The bulbs contract strongly and rapidly, beginning usually at the anal commissure and progressing some distance anteriorly. Any given section of the lateral vessels, however, may initiate short waves of contraction of its own accord. An optical section of a lateral vessel shows structure which apparently comprises transverse partitions, dividing the vessel into chambers. However, by focusing above and below the plane, it can be shown that these are not septa but only the infolded edges of the vessel wall. The cavity of the vessels is thus continuous. Occasionally minute granules are seen floating about in the fluid which fills the vessels. No blood cells could be identified, using the technique available.

The simple type of circulatory system found in *C. c. imminuta* and in other members of the genus *Carcinonemertes*, lacking the dorsal vessel, a condition found in only one other hoplonemertean, *Balaenanimertes chuni* Bürger (1909, p. 211), forms a striking contrast with the greatly ramified blood vessels found in the commensal nemertean *Malacobdella grossa* (Müller), a description of which may be found in the work of Riepen (1933).

*Excretory System.*—The excretory system in *C. c. imminuta*, and indeed in the entire genus, if it exists as a morphological unit, is unknown. The writer was unable to discover any trace of an excretory apparatus, either in the live worms or in sections. The absence of an excretory system is not confined to this genus. The pelagic *Polystilifera* (*Pelagoneustes*, *Nectonemertes*, etc.) lack this apparatus, and probably also

does the monostiliferan, littoral genus *Prosodenoporus*. However, future cytological investigations may demonstrate the existence of such a system. This was the case in *Cephalothrix*, which was believed to lack nephridia, until Coe (1930) demonstrated the presence of metanephridia probably homologous to those of the annelids.

*Nervous System.*—The nervous system consists of a four-lobed brain (fig. 20, B), embedded in the parenchyma near the anterior end of the body. From this arise two lateral nerve cords (fig. 20, LN). These extend posteriorly along the sides of the body in the parenchyma between the intestine and the submuscular glands (figs. 14, 17, 18, and 19, LN), and finally unite in an anal commissure (fig. 15, NC) ventrally to the terminal part of the intestine. The brain is composed of four ganglia, a dorsal and a ventral ganglion on each side, united dorsally and ventrally by commissures (fig. 16, VC and DC). Thus there is formed the brain ring, about  $20\ \mu$  in diameter, through which the proboscis and blood vessels pass. The esophagus lies directly below the ventral commissure.

In the living worms the brain lobes, situated a short distance posteriorly to the ocelli, are transparent to whitish, occasionally light flesh colored, with fine longitudinal striae. In eight worms the lobes varied from  $65$  to  $106\ \mu$  in diameter, averaging  $83\ \mu$ . The dorsal and ventral commissures are approximately  $38\ \mu$  in width, measured in an anterior-posterior direction. From the anterior faces of the dorsal ganglia there arises on each side a nerve (fig. 20, ON) about  $9\ \mu$  in diameter, which passes anteriorly to supply the head region and ocelli, which are embedded in the tissue of the head. These ocellar nerves, situated about  $60\ \mu$  apart, can be followed for only a short distance, usually about  $20\ \mu$ , when their branches become lost to view in the opaque parenchyma and gland cells. The ventral lobes of the brain taper rather sharply posteriorly to form the lateral nerve cords (fig. 48, LN). These, measuring  $13\ \mu$  in diameter, can be followed several hundred microns posteriorly, but become increasingly difficult to distinguish because of the obscuring submuscular glands, gonads, and intestinal pouches. There is no dorsal nerve, and the writer was unable to identify morphological units of any other sensory structures.

*Female Reproductive System.*—In the female the reproductive system is very simple, consisting merely of a series of sacs alternating with the intestinal lobes (fig. 34) and reaching from a short distance behind the anterior end of the intestine to the posterior end of the body. Each sac is bounded anteriorly and posteriorly by the intestinal pouches, while ventrally, dorsally, and laterally it is contiguous with the submuscular glands. When the ovaries are ripe and distended with developing eggs, the submuscular glands may be pushed aside and the walls of the ovaries brought into contact with the longitudinal muscle layer. The ovaries

at the extreme ends of the series are smaller and not as productive as the others. As may be seen in Table 4, the number of ovaries varies directly with the length of the worm. An adult worm 0.420 by 0.098 mm had 8 ovaries on the left side and 7 on the right, while a large mature worm 35.0 by 0.3 mm had 185 pairs of ovaries. The stage of development reached by the eggs of each ovary is nearly uniform throughout the body of any one individual, although there is some variation in this respect.

Some ovaries were seen which were nothing but large, thin-walled sacs, the lumen of which was empty of all solid materials (fig. 49). Evidently the eggs had just been shed from these ovaries, although no trace of ruptures or ducts to the exterior of the worm could be seen.

As already mentioned, worms taken from the gills of the crabs often show rudimentary gonads, in which little differentiation of the ovaries has occurred. In sectioned material they are seen to be solid clusters of cells. Sexually ripe worms, however, have sac-like ovaries, in whose walls the oogonia are situated. In the lumen of the sac can be seen eggs in the 1, 2, 4, 8, and sometimes 16 celled stage. McIntosh (1873-1874, p. 93) stated that in *C. c. carcinophila* he found ciliated embryos within the body of the parent worm, but this condition was not seen by the writer in *C. c. imminuta*. The number of eggs in any one ovary ranged from 1 to 7, with many younger eggs still in the walls of the ovary.

*Male Reproductive System.*—Since a detailed description of the male reproductive system in the genus *Carcinonemertes* was published (1941b) by the writer in the Journal of Morphology, only a brief account of the male system in *C. c. imminuta* will be given here. From each of the numerous oval testes which lie in the space between the intestinal wall and the submuscular glands there arises a delicate duct, the vas efferens. The many vasa efferentia are directed toward the mid-line of the body just dorsal to the intestine, where they empty into a long median duct, the vas deferens. Near the posterior end of the body the narrow vas deferens enlarges to form a seminal vesicle, filled with spermatozoa. At the posterior end of the seminal vesicle the vas deferens resumes its former narrow diameter, makes a loose single loop, and passes to the dorsal side of the posterior end of the intestine. There the vas deferens empties into the lumen of the intestine, forming in reality a cloaca. Spermatozoa are present throughout the male system. There is a thick ridge of cells projecting centrally from the mid-dorsal part of the body wall which accompanies the vas deferens from its anterior origin to the beginning of the seminal vesicle. It is present only in male worms and its function is not certainly known. Since Takakura (1910) was the first to recognize the existence of this unique male reproductive system, the writer proposes to refer to the vas deferens with its efferent ducts



as Takakura's duct. This type of male reproductive system is present only in the genus *Carcinonemertes* among the Nemertea. The writer has found no evidence for the support of Takakura's hypothesis that the vas deferens is a part of the proboscis which has become pinched off from the small anterior part and has come to serve another function. Takakura's duct is evidently in no way homologous with the posterior part of the proboscis, but is a structure of separate origin.

*Distinctive Characters of C. c. imminuta.*—*Carcinonemertes carcinophila imminuta* differs from *C. c. carcinophila* (Kölliker) in its smaller size, shorter and more slender basis, and shorter stylet. A tabular comparison of the two closely related varieties is given in Table 7. Although the differences appear at first glance to be minute, they have been studied in great detail and have been found to be constant. It should be noted that there is no significant difference in the ratio of stylet to basis.

#### DEVELOPMENT AND BIONOMICS

In discussing this topic references will be freely made for the sake of completeness to work published on other members of the genus, especially *C. c. carcinophila*. The latter is so closely related to the variety under immediate consideration that any data regarding it should be taken into account.

*Copulation and Insemination.*—The process of copulation, leading to the fertilization of the eggs, has been described in this genus by Coe (1904a, p. 552) as follows: "In *Carcinonemertes* a number of writers have observed the male and female worms to place their bodies side by side, either in an outstretched condition or somewhat folded, and then to secrete a large amount of mucus which encloses the bodies of both worms in a common mass of secretion. The eggs are then deposited from both sides of the body of the female and are fertilized by the sperm discharged simultaneously by the male. Sometimes several of each sex,

TABLE 7.—COMPARISON OF *C. c. imminuta* WITH *C. c. carcinophila*

	<i>C. c. imminuta</i>		<i>C. c. carcinophila</i>	
	Extremes	Average	Extremes	Average
Length of basis. . . . .	19–23 $\mu$	21.0 $\mu$	19–30 $\mu$	25+ $\mu$
Diameter of basis. . . .	4.5–6 $\mu$	5.3 $\mu$	6–8 $\mu$	7 $\mu$
Stylet length. . . . .	6–9.5 $\mu$	7.3 $\mu$	6–12 $\mu$	9 $\mu$
S:B ratio. . . . .	0.272–0.461	0.347	0.316–0.400	0.358
Body length. . . . .	0.42–35.0 mm	about 15 mm	20–70 mm	about 30 mm?

sometimes a single male and a single female participate in this act. If it happen that a portion of the eggs in any of the ovaries are retained within the body of the female, such eggs are fertilized by spermatozoa which enter the openings into the ovaries." The process of copulation and ensuing insemination was not observed by the writer in live worms. In fact, during the course of the numerous observations, a male and a female were never seen together in the same mucous sheath. It seems probable that this does occur, however, since otherwise sufficient numbers of spermatozoa would be unlikely to locate the female on account of the dilution of the spermatozoa in the sea water. That males and females in this genus do at times occur together in the same sheath is beyond doubt, for in sections of the new species to be described below there is one which shows both sexes in the same sheath.

The great numbers of spermatozoa present in the seminal vesicle of the male are probably forced out through the anus by the contractions of the body wall, the vesicle itself undergoing no contractions. The mucous sheath surrounding the two animals retains the spermatozoa in close proximity to the female, whose ovaries they then enter.

*Early Cleavage Stages.*—The eggs are formed in the walls of the ovary and later come to lie free in the lumen of the ovarian sac (fig. 17, O). The walls of the latter contain both oogonia in various stages of development and yolk granules (fig. 17, W). Unfertilized eggs are infrequently seen. One such egg measured  $58\ \mu$  in length and somewhat less in width (fig. 37). Its cytoplasm was very finely granular. Its clear transparent nucleus, measuring  $17\ \mu$  in diameter, contained a grayish body (nucleolus)  $8\ \mu$  in diameter. The cell membrane was the only external covering. Fertilized eggs (fig. 38), possessing a thin hyaline fertilization membrane, measured  $55\ \mu$  in diameter with grayish nuclei (fusion nuclei)  $16\ \mu$  in diameter. The cytoplasm was more coarsely granular than previously with numerous small vacuoles. Van Beneden (1861, Pl. III, figs. 14 to 16) and McIntosh (1873-1874, Pl. 17, fig. 19) have both given drawings of the eggs of *C. carcinophila*.

The two-celled stage (fig. 45), measuring  $63$  by  $43\ \mu$ , with nuclei  $12\ \mu$  in diameter, has cytoplasm and nuclei similar in texture to the one-celled stage. The second cleavage plane, at right angles to the first, divides the egg into four equal blastomeres (fig. 39), each about  $33\ \mu$  in diameter, with nuclei  $5\ \mu$  in diameter. The egg, measuring approximately  $71$  by  $50\ \mu$ , is now flattened in a polar direction (fig. 10).

The third cleavage plane is equatorial (fig. 8) and divides the egg into eight blastomeres, each  $26$  to  $27\ \mu$  in diameter, with minute nuclei which cannot be definitely made out in the living state. The upper four blastomeres lie in the grooves between the four lower ones, indicating

that the cleavage is probably of the spiral type. The egg has now regained its original spherical shape. The blastula (fig. 46), containing numerous small blastomeres 12 to 13  $\mu$  in diameter, measures 78  $\mu$  in total diameter. No embryos beyond the blastula stage were seen in the body of the parent worm. Succeeding stages were all outside the body. According to McIntosh (1873-1874, pp. 93-94) the embryos of *C. carcinophila* are sometimes retained in the body of the female. He wrote, "Many of the parents with developing young in their interior are feeble, and almost in a decaying condition inside the sheaths, so that the inert bodies seem but the nidi for the growth of their progeny . . . ."

*Late Embryos and Egg Cords.*—The embryos, still inside the egg membranes, are shed by the mother worm and are cemented to the inner surface of the walls of the mucous sheath by mucus, which hardens in the water to hold the eggs firmly in place. The worm then retreats from that area of the sheath, and the latter collapses to form a solid cord of eggs (fig. 21), each egg containing a developing embryo. All the embryos present in one egg cord are in nearly identical developmental stages, indicating that they were all extruded from the same female worm at about the same time. Both Van Beneden (1861, Pl. III, figs. 17 and 18) and McIntosh (1873-1874, Pl. 16, fig. 18) showed embryos in the egg cords of *C. carcinophila*.

The embryos soon develop cilia and ocelli, and begin to rotate inside their egg membranes (fig. 44). However, the embryos in some eggs may not show ocelli until they reach the free-swimming stage. The diameters of 20 eggs gave an average diameter of 75  $\mu$ , with extremes of 67  $\mu$  and 84  $\mu$ . These embryos possessed two irregularly shaped ocelli, 3.6 by 5.4  $\mu$ . They rotated for 60 hours in a finger bowl of sea water at a temperature of about 80 degrees Fahrenheit, after removal from the egg mass of the crab. The addition of clean water caused the embryos to speed up their rotations. Normally in clean sea water they rotated once every two seconds. No internal differentiation of structure other than the ocelli could be seen in the living specimens. The body is grayish and filled with numerous globules and granules of various kinds. McIntosh (1873-1874, p. 93) stated that in *C. carcinophila* "the embryo in each is sometimes ciliated on the tenth day (Pl. 16, fig. 20), although entire dependence cannot be placed on this date, since development occurs within as well as without the body of the parent." The embryos lie uncoiled in the egg membranes. Bulging movements at each end of the embryo rupture the delicate surrounding membranes and the embryo, now a free-swimming larva, swims forth with its cilia beating rapidly.

*Free-swimming Larva.*—Immediately after hatching, the body is spherical and of the same size as it was while in the egg. The cilia beat



rapidly and the anterior cirrus, located terminally, whips around actively. Soon, however, the larva elongates (fig. 25), and the posterior cirrus can be plainly seen on the terminal part of the body. The anterior and posterior cirri are evidently formed while the embryo is still in the egg membranes, but they are not evident until after hatching. The larvae spiral in their course, all the while being propelled ahead in a zigzag line. The two cirri wave back and forth during swimming, and the cilia beat continuously. Swimming is accomplished by means of both cilia and cirri. The movement of the cilia accounts for the rotating motion, like that of a ciliate protozoan, while the whipping back and forth of the cirri accounts for the zigzag movement, resembling that of a flagellate protozoan. The anterior cirrus is about twice as long as and more active than the posterior one. The measurements of five free-swimming larvae are shown in Table 8. Most of the larvae are slightly flattened dorso-ventrally. One larva, 134 by 64  $\mu$ , contracted under pressure to a spherical shape with a diameter of 84  $\mu$ , possibly indicating that muscle fibers are already differentiated at this early stage. The cilia covering the body measure 6  $\mu$  in length, or about the same length as in adult worms. Each cirrus is made up of at least three long thread-like elements which normally work in unison as one cirrus (fig. 5). Under pressure the elements sometimes become separated. The cirri were first mentioned by Van Beneden (1861, p. 22), but nothing was known of their multipartite nature.

In living larvae very little structural differentiation can be seen. The two brownish yellow ocelli, which may be very minute (only 1 or 2  $\mu$  in diameter) or altogether absent, are made up of clusters of small granules. In a larva 130 by 70  $\mu$ , the ocelli were located 18  $\mu$  apart at a level 22  $\mu$  from the anterior end of the body. The larva is covered with a ciliated integumental epithelium about 7  $\mu$  in thickness.

Many writers have gone on the assumption first made by Van Beneden (1861, pp. 22-23) that in *C. carcinophila* the outer ciliated coat is

TABLE 8.—MEASUREMENTS (IN MICRONS) OF FREE-SWIMMING LARVAE OF *C. c. imminuta*

Length	Width	Anterior Cirrus	Posterior Cirrus
126	97	50	25
138	100	60	34
105	46	28	13
134	64	46	24
130	70	41	20
126.6	75.4	45	23.3

shed before the definitive worm appears. Van Beneden's account of this was as follows:

Les cils vibratiles sont devenus maintenant si nombreux, qu'ils forment une toison autour du jeune ver, toison qui tombe aussitôt après et emporte le filament qui semble lui avoir servi de sentinelle au début de la vie. Le jeune ver, après cette mue, n'a pas changé de forme, conserve les deux points oculaires et n'a subi d'autre changement que celui de la perte de l'organe exploratif dont nous ne nous de parler. C'est le moment de nous demander: est-ce une mue que le ver subit ou bien est-ce un scolex qui a engendré un proglottis? Nous penchons fortement en faveur de cette dernière interprétation, d'autant plus que l'analogie des vers distomes, aussi bien que des cestoides, lui est favorable. La première forme, avec ses deux filaments à un ou deux pôles, représente l'enveloppe ciliée des jeunes distomes à leur éclosion, et la vésicule hexacanthé du premier âge des Cestoides, ou enfin les Pilidium, étudiés avec tant de soin l'année dernière par MM. Leuckart et Pagenstecher.

The same author showed a figure (Pl. III, fig. 28) of a three-day old larva ("embryon, âgés de trois jours") which has lost the outer coat of cilia supposedly and the cirri.

Concerning the shedding of the ciliated epithelium, McIntosh (1873-1874, pp. 93-94) wrote:

[Van Beneden] fell into the error of supposing that a form having a smooth outline was developed within its progenitor with the long ciliary tuft, the former representing the *scolex*, and the latter the *proglottis*; in short, as he says, a case of digenesis, and not a metamorphosis. But his drawing represents the so-called *proglottis* furnished with two eyes exactly in the same manner as the *scolex*, yet he neither mentions having seen the one form inside the other nor figures this interesting condition. No such mode of development has ever been seen by me, either in the case of those ova deposited in the unimpregnated condition or in those developed within the body of the parent; but the same gradual changes ensue in the young of this animal as in *Tetrastemma*, and, as will afterwards be seen, also in *Cephalothrix*.

Dieck (1874) claimed that in *Cephalothrix galathea* Dieck (? = *C. carcinophila*) the larval integument with its cilia and cirri is shed.

Since the writer was unable to keep the free-swimming larvae alive in the laboratory until they settled down to a crawling existence, no observations on the morphological changes could be made. One thing is certain, however, that the anterior and posterior cirri are lost during the metamorphosis. The smallest crawling worms seen showed no traces of them. The whole subject of metamorphosis in this species is one which urgently requires investigation. At present McIntosh's interpretation, based as it is upon actual observations, seems to the writer to be more reliable than any other.

The granular interior of the larva contains in the posterior region numerous clear globules measuring  $4\ \mu$  in diameter. Smaller globules of various sizes are scattered through the body. A clear bilateral area posterior to the ocelli probably represents the brain rudiments, while an indefinitely defined central area indicates the position of the esophagus and proboscis. Van Beneden (1861, Pl. III, fig. 28) mistook the esophageal region in the European *C. carcinophila* for the mouth.

When a heavily infested egg mass of a crab is placed in a finger bowl of sea water, thousands of free-swimming larvae emerge within an hour or two from among the crab eggs and swim to the side of the dish nearest the source of light. They are, then, positively phototactic, in contrast to the negative phototaxis of the adult worms. The larvae did not survive more than a day or two, even with many changes of water. The unavoidably high temperatures in the laboratory in which they were kept, ranging from 70 to 95 degrees Fahrenheit, probably were a factor contributing to their mortality.

*Immature Worms.*—Very minute worms, negatively phototactic like the adults, were found crawling about on the egg masses of the crab. These were more numerous on the older, dark brown or black egg masses than on the younger, light yellow or orange eggs. The smallest, taken from an orange egg mass, measured 300 by 88  $\mu$ . The intestine, filled with a brownish, granular material, was a simple sac with no lateral pouches. The ocelli were very irregular in shape, and not distinctly separated. The basis measured 20 by 5  $\mu$  and the stylet 5  $\mu$  in length. Unfortunately this specimen was crushed before a camera lucida drawing could be made.

Another worm (fig. 20), measuring 0.378 by 0.126 mm under pressure of a cover glass and 0.273 by 0.084 mm without pressure, had a basis 21 by 5.5  $\mu$  and a stylet 6  $\mu$  long. The body was highly contractile. There were two ocelli 13 and 19  $\mu$  in diameter respectively. Brain, lateral nerve cords, blood vessels, intestine, and esophagus were all completely formed though not of mature size. No traces of gonads could be seen. The middle proboscis chamber was 15  $\mu$  in diameter and the posterior chamber 38 by 19  $\mu$ .

A third immature worm, 336 by 155  $\mu$ , had four irregular ocelli, each 8 to 9  $\mu$  in diameter. The basis and stylet were not well formed. The proboscis chambers were distinct, however. The intestine was a brownish, central mass, and the brain lobes were conspicuous.

Between the sizes of the largest free-swimming larva (138 by 100  $\mu$ ) and the smallest immature worm observed (278 by 84  $\mu$ ) there must occur a great deal of differentiation of organs in the body. The alimentary canal, proboscis, nervous, circulatory, and muscular systems are all formed almost completely during that time, although rudiments of these systems are probably present early in the free-swimming larva or even in the unhatched embryo.

The smallest sexually mature female worm observed (fig. 34) was 0.420 by 0.098 mm. Its sheath was creased longitudinally and had no raised lapilli. Several eggs were scattered along the inner wall of the sheath and many more were present in the body of the worm. The smallest adult male worm observed was 0.928 by 0.131 mm. Although the worms may mature at the small sizes just mentioned, the length of



the body continues to increase. Worms from the gill lamellae of the crab ranged from 0.777 to 33 mm. In many of them rudiments of gonads could be seen when observed in the living state. Sections of these worms showed the presence of immature gonads also.

Table 9 shows some of the growth changes which occur in the developing worms.

The ocelli increase in size. The middle proboscis chamber and the posterior proboscis chamber are noticeably smaller in the worms under 1.5 mm in length. In worms less than 1 mm the esophagus appears to be small and weak. The measurements of the basis and stylet in minute worms and large adults do not seem to differ much. In correspondence with the writer (November 8, 1940) regarding the size of the basis in nemerteans, Dr. Coe wrote: "I have found during recent years the most surprising differences in the size and proportions of stylet and basis in individuals of different ages and size in the same species. By experimental studies I find that the basis and all accessory stylets are sloughed off from time to time during growth and replaced by those of longer size as growth proceeds. There is a general correlation between size of worm and size of basis but it is not always very close." Whether such is the case in *C. c. imminuta* is not known, and the observations of the writer show nothing to substantiate such a course of events. In fact, the data

TABLE 9.—MEASUREMENT OF GROWTH CHANGES IN *C. c. imminuta*

Length (mm)	Width (mm)	Basis ( $\mu$ )	Stylet Length ( $\mu$ )	Diameter of Ocelli ( $\mu$ )	Diameter of Middle Proboscis Chamber ( $\mu$ )	Posterior Proboscis Chamber ( $\mu$ )	Esophagus ( $\mu$ )
0.300	0.088	20 x 5.0	5.0	...	...	.....	.....
0.378	0.126	21 x 5.5	6.0	13, 19	15	38 x 19	.....
(0.278 x 0.084 without pressure)							
0.573	0.180	22 x 4.5	5.5	17	...	.....	35 x 28
0.629	0.164	22 x 5.0	6.0	28	24	37 x 37	distinct
0.647	0.233	20.5 x 4.5	6.5	...	10	18 x 18	.....
(0.518 x 0.148 without pressure)							
0.740	0.259	22.5 x 5.5	6.0	20	17	22 x 17	.....
0.777	0.150	22 x 5.5	6.5	...	...	.....	.....
0.814	0.222	21 x 5.5	6.0	...	...	.....	.....
1.100	0.190	21 x 5.5	7.0	...	...	.....	weak
1.220	0.140	22 x ...	6.0	20	38	85 x 70	147 x 120
1.387	.....	20 x 4.0	7.0	13	...	.....	.....
1.424	0.095	21 x 4.5	5.0	5	...	84 x 67	138 x 151
10-20	0.300	21 x 5.3	7.3	20-70	35	139 x 47	178 x 97

available indicate that the basis and stylet are formed early in development and apparently at their maximum size.

*Morphology and Life History of the Host, Callinectes sapidus.*—A brief account of the morphology and life history of the blue crab, *Callinectes sapidus* Rathbun, is necessary here in order to bring in information relevant to the elucidation of the life history and host relationships of *C. c. imminuta*. It is upon this crab that the nemertean lives commonly at Grand Isle, Louisiana.

The branchial chambers of *Callinectes sapidus* are morphologically a part of the exterior of the body. The dorso-lateral edges of the carapace covering the thorax have been extended laterally and ventrally, meeting the bases of the walking legs so as to enclose the gills in cavities shut off from the outside world, except for inlets and outlets for water. Each gill has the shape of an elongated pyramid and consists of 200-300 separate lamellae, to which the venous blood is carried by the dorsal afferent veins. Each lamella of the eight pairs of gills is covered with a thin layer of chitin which is continued over the outside of the afferent and efferent blood vessels. The lamellae are ornamented with various projections along the outside edge (text fig. 2), which serve to keep the lamellae separated from one another. The gill chitin is continuous with the chitinous covering of the body, and as such is cast off at each ecdysis. Nemerteans encapsuled between the lamellae are cast off also. This was demonstrated by the writer by infesting young crabs with nemerteans which had been previously stained with Nile blue sulphate, after the method of Loosanoff (1937) and Vernon (1937). The stained worms were found on the gills of the exuvium.

The water enters the gill chambers, according to Truitt (1939) and the writer's observations, through slits at the bases of the chelipeds, and, after passing over the gills, is forced out of the chamber through the exhalent opening above the bases of the second maxillae. The three flabella (epipodites) of the maxillipedes assist the scaphognathite in its action of baling out water from the gill chamber.

Solid particles are often found in the gill chambers. Grains of sand, many commensal barnacles (*Octolasmis mülleri* (Coker)), bryozoans, and in one case a specimen of *Nereis* 3 cm in length have been found by the writer.

The gill chambers afford a splendid habitation for the animals which live there. They are protected from their enemies of the outside world, have abundant food and dissolved gases for respiration brought to them, and their waste products are carried off. The chief disadvantages are that they live only as long as the host lives and that they are thrown off the host when the crab molts.

The first two abdominal segments of the adult male bear specialized appendages. In the adult female there are four pairs of pleopods, bearing long hairs. The eggs of the crab are attached only to the hairs of the endopodites, never to those of the exopodites. The mechanism of the attachment of the eggs in a related crab has been described by Yonge (1938). When the crab has come into "berry," i.e., when it is ovigerous, the abdomen is extended posteriorly, and the pleopods wave back and forth almost constantly. The eggs when first laid are light yellow to orange, but as the chromatophores of the crab embryos develop the whole egg mass becomes dark brown or almost black in some cases.

The most thorough investigation of the life history of *C. sapidus* is that of Churchill (1919), conducted at Chesapeake Bay, Maryland, which combined data from Binford (1911) and included much new material. The crab embryos require about fifteen days to hatch from the eggs attached to the pleopods of the mother. The ensuing free-living zoea and megalops stages occupy about one month. From the megalops to the adult about fifteen moltings occur, with an average time between molts of 15 days, ranging from 6 days for the early stages to about 25 days for the last. The crabs become mature and mate during the second summer, when about 12 to 14 months of age. The female does not molt after reaching sexual maturity. The spermatozoa she received during copulation at her last molting suffice to fertilize two or more successive lots of eggs. The usual life span is probably about three years. During copulation the male carries the female about and holds her for hours or sometimes even days (Chidester, 1911).

In a statistical study of molting in *C. sapidus* in Chesapeake Bay, Maryland, Gray and Newcombe (1939) found that, starting with the initial size of 20 mm in width, the male crabs molted eleven times, two more than the number for females of the same initial size. The latter apparently do not molt after becoming sexually mature, while the males undergo at least two additional molts.

*Callinectes sapidus* is found from Nova Scotia (Piers, 1933) to Uruguay (Rathbun, 1930). It is extremely abundant in the region of Grand Isle, Louisiana, being by far the most commonly found of the larger invertebrates, with the exception of the oyster which is cultivated there. It is more abundant throughout its range in estuaries, where it sometimes invades brackish or even fresh water. Gunter (1938) found an immature male in the Atchafalaya River at Simmesport, Louisiana, on August 4, 1937, a locality 160 miles from the Gulf of Mexico.

The blue crab will live out of water only a short time. Pearse (1928-1929) reported 28.5 hours as the maximum time in air and again (1936) reported an average out of 14 crabs of 34.4 hours and a maximum of 97.3.

Churchill (1919) observed that the females migrate to water of



higher salinity when ready to lay their eggs. After the young are hatched, the females may migrate back to the fresher water. The males tend to remain in the shallow regions of rather low salinity, where they copulate with the virgin females which are constantly arriving from the regions of higher salinity. In the winter the females and probably a good many of the males also go to deeper waters (Churchill, 1919, and Cowles, 1930) where they lie dormant on the bottom. Nothing is known regarding the extent or rapidity of migration in *C. sapidus*. The tagging experiments of Meek (1913) showed that in England the common crab, a close relative of *C. sapidus*, may migrate as much as 28 miles in 36 days, a considerable speed and distance. Such migrations would bring about widespread distribution of any nemerteans which the crabs might be carrying at the time.

The area in which the specimens of *C. sapidus* were collected comprised about 400 square miles in the vicinity of Grand Isle, Louisiana. Grand Isle separates the island-dotted Barataria Bay from the Gulf of Mexico, except for the various passes, Caminada Pass, Barataria Pass, or Grand Pass as it is sometimes called, Quatre Bayou Pass, and other smaller ones. The depth of the water in Barataria Bay seldom exceeds 10 feet, although in the passes to the open Gulf it may reach 60 feet. Much of the bottom in the bay, composed of sand and silt, is devoted to oyster culture. Innumerable shallow mud flats and marshy inlets are found around the islands. Outside in the Gulf proper the bottom is predominantly sandy, with still a good proportion of mud near the shore. The turbidity is much less than in the bay region. The pH range, determined in the field colorimetrically, of samples from Barataria Bay and from offshore in the Gulf was 7.6 to 8.4. The bottom in the Gulf slopes off from Grand Isle very gradually until about three miles offshore, when the slope becomes much steeper. At three miles the depth is only about 15 to 20 feet, while at twelve miles it reaches 40 to 50 feet. The temperature of the water ranged from 25.8 to 29.8 degrees Centigrade. The salinity, determined by the silver nitrate titration method as outlined by Johnstone (1928), was progressively higher as one proceeded from the extreme northern reaches of the bay toward the Gulf. At Chene Fleurie in the extreme northern part of Barataria Bay the salt content was only 9.18 grams per liter. Southward in the bay near Manila village the salinity was 19.23, at Bayou Fifi at the eastern end of Grand Isle it was 25.30, and five miles south of Grand Isle it was 29.32 grams per liter. The specific gravity varied correspondingly with changes in the total salt content (True, 1915). The readings of both salinity and specific gravity were checked by the formulae and tables given by Knudson (1901).

*Life History of C. c. imminuta.*—The writer was unable to demon-

strate the life history of this nemertean in the laboratory because of the brief time available for work at Grand Isle and because of the lack of suitable laboratory apparatus for maintaining crabs and worms alive. However, by fitting together statistical information on infestations in the crabs and observations of the various immature stages of the worms with the life history of the crab, some deductions can be made which reveal in a general way the life history of this nemertean.

The time required after fertilization before extrusion of the developing eggs from the body of the female is unknown, but is probably only a few days. McIntosh (1873-1874) believed that the eggs in the egg cords of the European *C. carcinophila* require about ten days before hatching occurs. During that time the egg cords are waved about and kept clean of other organisms and debris by the movements of the pleopods. The time for hatching of *C. c. imminuta* is probably shortened in the warm Gulf waters. The free-swimming larvae hatch from the egg by making bulging movements which rupture the egg membranes. After a short time the larvae begin to elongate and the anterior cirrus, present when the larva is hatched from the egg, is followed by the appearance of a posterior cirrus. The eye spots, often present in embryos while still in the eggs, are nearly always present in the free-swimming larvae. The larvae swim actively about, and are capable of scattering over a considerable area by their own movements. A large proportion of the larvae are probably washed away from the egg mass of the host crab by the currents set up by the beating of the pleopods. The escape from the host egg mass and wide distribution in the water may be aided by the positive phototaxis of the larvae. The ventral side of the crab abdomen among the eggs is dark in comparison with the brighter surrounding water. Then, too, the surface water is more brightly lighted than the water near the bottom. The larvae therefore are doubtless stimulated to swim out from the egg mass and toward the surface of the water. There they may come in contact with (1) the gills of immature male crabs, (2) the gills of mature males, (3) the gills of immature females, (4) the gills of mature females, or (5) the egg masses of adult females. Some of the larvae may remain on the original egg mass and develop into the crawling worms there. Van Beneden (1861) stated that in the European *C. carcinophila* the embryo three days old, i.e., the free-swimming larva three days old, has then already lost its cirri and settled down to a crawling existence.

The shallow water, the relative lack of strong currents in the Barataria Bay region, and the abundance of crabs (in some areas estimated to be at least one crab in every 100 square feet of bottom) all seem to aid the larvae in coming in contact with the bodies of crabs which are potential hosts.

The time required from fertilization until the hatching of the free-

swimming larvae from the eggs (about 11 days) is well within the time required for the crab eggs to hatch (about 15 days). The period of about three days needed for development of the free-swimming larvae before they settle down to the definitive crawling state, added to the previous time makes a total of about 14 to 15 days from fertilization until the larvae are capable of infesting other crabs. This time, necessary for the development of the worms, is probably considerably shortened in the warm waters of the Grand Isle region.

The fate of the free-swimming larvae varies. Many of them probably never come in contact with a suitable crab host, and eventually die. Some of them, no doubt, are eaten by fish and various invertebrates. Those which do succeed in reaching a crab have only about two chances out of five of its being one on which they can become mature, i.e., an adult female either with or without an egg mass.

In order to determine the incidence of the nemerteans on *C. sapidus* and the correlation with sex, age, and molting, 819 crabs of both sexes and in various stages of maturity were examined during the months of June and July in the vicinity of Grand Isle in 1939 and 1940. The results are shown in Tables 10 and 11.

Table 10 shows that the immature male crabs were uninfested with *C. c. imminuta*, although one such crab had *Octolasmis mülleri* (only a single specimen, however, and that not mature). The adult males, i.e., those over 89 mm in width, according to the standard of Gray and Newcombe (1939), showed a light infestation with the barnacles in about 18% of the total number examined. Those males from the Gulf were more frequently infested with barnacles than those from Barataria Bay. In each individual the infestation never exceeded 20 barnacles. The number was usually much less, and often those present were immature. Two mature males had a few minute nemerteans on their gills. These were all less than 1 mm in length. The smallest mature male crab infested was 10.9 mm in total spine to spine width. One of the worms recovered from its gills was 0.573 by 0.180 mm. The total percentage of males infested was only 0.97%. A single male had both barnacles and nemerteans in the gill chambers.

The immature female crabs were likewise extremely lightly infested. One such crab had a single nemertean, two others had both nemerteans and barnacles, while two more had only barnacles. The infestation by both worms and barnacles was very light. The smallest infested immature female crab was 9.1 mm in total spine to spine width. The smallest worm recovered from the gills of an immature female was 0.777 by 0.150 mm and none exceeded 1.5 mm in length.

These incidence data may be interpreted easily by recalling the known facts of the life history of *C. sapidus*. The younger the crab is, the



TABLE 10.—INCIDENCE OF *C. c. imminuta* AND *O. mülleri* ON *C. sapidus* AT GRAND ISLE, LOUISIANA, AND THE CORRELATION WITH SEX, AGE, AND MOLTING

	Immature Males		Mature Males		Immature Females		Mature Females without Eggs		Mature Females with Eggs	
	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent	Num-ber	Per-cent
Crabs examined:										
In Bay.....	10	.....	118	.....	42	.....	79	.....	49	.....
In Gulf.....	4	.....	87	.....	29	.....	297	.....	104	.....
Total.....	14	.....	205	.....	71	.....	376	.....	153	.....
<i>C. c. imminuta</i> only on gills:										
In Bay.....	..	.....	1	0.85	1	2.38	6	7.59	3	6.12
In Gulf.....	..	.....	1	1.15	..	.....	28	9.42	10	9.62
Total.....	..	.....	2	0.97	1	1.41	34	9.04	13	8.49
<i>O. mülleri</i> only on gills:										
In Bay.....	..	.....	6	5.08	2	4.76	8	10.12	4	8.16
In Gulf.....	1	25.00	30	34.47	..	.....	36	12.12	4	3.84
Total.....	1	7.14	36	17.56	2	2.82	44	11.70	8	5.23
Both <i>C. c. imminuta</i> and <i>O. mülleri</i> on gills:										
In Bay.....	..	.....	1	0.85	2	4.76	28	35.44	2	4.07
In Gulf.....	..	.....	..	.....	..	.....	78	26.26	8	7.69
Total.....	..	.....	1	0.48	2	2.82	106	28.19	10	6.53
<i>C. c. imminuta</i> on eggs only:										
In Bay.....	..	.....	..	.....	..	.....	..	.....	11	22.45
In Gulf.....	..	.....	..	.....	..	.....	..	.....	4	3.84
Total.....	..	.....	..	.....	..	.....	..	.....	15	9.81
<i>C. c. imminuta</i> on both gills and eggs:										
In Bay.....	..	.....	..	.....	..	.....	..	.....	31	63.26
In Gulf.....	..	.....	..	.....	..	.....	..	.....	16	15.38
Total.....	..	.....	..	.....	..	.....	..	.....	47	30.71

shorter is the period between molts, and the less the opportunity for the worms and barnacles to become established on the gills, since the worms and barnacles live on the exterior of the chitinous covering of the body and are thrown off at each molt. This interpretation agrees with the fact that worms and barnacles were found only on immature crabs of large sizes, and also with the fact that the infestation by barnacles was higher in the mature males than in the immature ones. It will be remembered that Gray and Newcombe (1939) found that the male crabs continued to molt after reaching sexual maturity. The longer time between molts in the mature males allows greater opportunity for the barnacles to become attached, hence the higher number of crabs infested. The nemerteans evidently are not able to live successfully in the gill chambers of male crabs, probably because of the shorter stadia, and probably also because of the tendency of the males to stay in the shallow, fresher water, sometimes in marshy pools, thereby diminishing the chances of the free-swimming larvae of coming in contact with them. The mature females, on the other hand, tend to migrate about and live in areas where the larvae can become readily disseminated. All males and immature females, of course, have no eggs, and this fact would prevent the worms from thriving on such crabs, if it is true, as the writer has concluded, that the worms feed on the crab eggs.

The mature females, in contrast to the males and immature females, are heavily infested with both barnacles and nemerteans. Of the 376 non-ovigerous females the gills of 140, or 37%, were infested with *C. c. imminuta*. Eighty-five, or 55%, of the ovigerous females were infested either on the gills or on the egg masses or both.

The non-ovigerous females showed no significant differences in infestation in Barataria Bay and in the Gulf proper. Combining the number of such crabs with nemerteans on their gills (34) with those

TABLE 11.—SUMMARY OF DATA ON INFESTATION OF *C. sapidus* WITH *C. c. imminuta* AT GRAND ISLE, LOUISIANA

Type of Crab	Number Examined	Number with <i>C.c.i.</i> on Gills or Eggs	Percentage of Number with <i>C.c.i.</i>
Immature males.....	14	...	....
Mature males.....	205	3	1.46
Immature females.....	71	3	4.23
Non-ovigerous mature females.....	376	140	37.18
Ovigerous mature females.....	153	85	55.55
<i>Totals</i> .....	819	231	28.20

which had both nemerteans and barnacles (106) it is found that of the total number of non-ovigerous females, 140, or 37%, were infested with nemerteans. The number of nemerteans on any one crab was almost always large. No attempt was made to count the worms. One crab was estimated to have at least 1,000 worms of various sizes between the lamellae in the two gill chambers. Another had 640 barnacles by actual count in the gill chamber of one side. In a previous article (1941a) the writer has shown that at Grand Isle, Louisiana, the nemerteans and barnacles associate with *C. sapidus* at random and that there is evidently no relationship between nemerteans and barnacles that would favor their occurrence together on the crabs or inhibit the occurrence of one after the other has become established. The data on *Octolasmis mülleri* has been included in this discussion because it tends to corroborate the findings regarding the nemerteans.

The ovigerous females showed a light infestation in the gill chambers (23 out of 153 crabs, or 15%) and a heavy infestation of the egg masses (62 out of 153, or 40%). This indicates that the worms may leave the gills when the crab comes into berry and attach themselves in sheaths on the endopodite hairs among the eggs, where their gonads rapidly mature, the eggs are fertilized, and embryonic development takes place. The data also show that the worms probably return to the gills when the eggs of the crab are all hatched, since 37% of the non-ovigerous females had gills infested with nemerteans, but only 15% of the ovigerous crabs were so infested.

The writer found no worms living on the abdominal endopodite hairs of crabs which were not carrying eggs, although Van Beneden (1861) stated that in his study of the European *C. carcinophila* he found one nemertean 3-4 cm in length living on the endopodite hairs of a crab without eggs.

The higher infestation on the egg masses of crabs from Barataria Bay (42 out of 153, or 27%) as compared with that in the Gulf (20 out of 153, or 13%) is probably brought about by the more favorable conditions (shallow water, lack of strong currents, abundance of crabs, etc.) for the contact of the free-swimming larvae with new hosts.

In order to become sexually mature the free-swimming larvae must reach either non-ovigerous or ovigerous adult female crabs. After the larva loses its anterior and posterior cirri, it crawls but never swims. When the egg mass of the new host is hatched, the young worms migrate into the gill chambers where they encapsulate between the gill lamellae (text figs. 1 and 2). Probably none of the recently transformed young worms reach maturity on the first egg mass with which they make contact, but remain on the gills until the next batch of eggs is laid by the



crab, when they migrate out to form their sheaths attached among the crab eggs to the abdominal pleopod hairs. Churchill (1919) has shown that in *C. sapidus* there may be at least two successive batches of eggs, one in the second summer of life and another in the following summer. After the last molt occurs, at which time the female crab becomes sexually mature, all the worms which settle upon the gill lamellae remain on the body of the crab, probably for the duration of the life of the crab, which is about three years, according to Churchill (1919). The number of worms is probably increased each time that the crab berries by the settling of some of the young worms upon their mother's host. From this reasoning one would expect to find the older female crabs, which have already had one batch of eggs, more heavily infested than females which never yet have been in berry. The writer is unable to substantiate this because it is impossible to tell whether a crab has already been ovigerous and infested. There is no correlation between the size of the adult female crab and infestation with nemerteans.

Churchill (1919) stated that in Chesapeake Bay "if mating occurs quite early in the season, the eggs are laid within about two months. In the great majority of cases, however, mating occurs in July or August and the eggs are not laid until the following spring or summer." In Louisiana, however, where the water is warmer, the development of the eggs after copulation is probably hastened. At any rate there is a period of nearly two months between the last molt and the first laying of the eggs, during which many nemerteans can become settled on the gills. Perhaps a good many of the uninfested, or very slightly infested, ovigerous females are those in which the first batches of eggs, laid in the same season in which copulation occurred, are being carried, and the more heavily infested ones are those which are carrying first batches of eggs which were laid the season following that in which copulation occurred or which are carrying second or third batches of eggs. Evidence for this is suggested by the observation that egg masses which are infested by large, mature worms are generally infested by a great many such worms.

Growth of the worms probably occurs while they are on the gills, because otherwise it would appear to be impossible to account for the large sizes attained. Even if the migration to the egg masses took place twice during the life of the worm, that would allow only about thirty days for the growth of the worm from less than 1 mm to over 30 mm in length, an event which seems physiologically improbable.

The worms on the gill lamellae secrete a mucous substance by which the two lamellae are cemented together around the worm (text figs. 1 and 2). The wall of the capsule thus formed is very fragile, and when the



gill is removed from the crab and placed in a finger bowl of sea water the worms begin to move about. In a few minutes they rupture the walls of the capsule and crawl out over the surface of the gills.

Sexually mature worms were found abundantly throughout the last part of May, all of June and July, and the first part of August of the years 1938, 1939, and 1940. A few records of crabs collected in Barataria Bay during the winter months are shown in Table 12.

Although these data are scanty, they do show that the crabs in the Barataria Bay region are in berry nearly as late as the first of November and as early as the last part of March. (The brown eggs on the two females collected on April 7, 1940, must have been laid at least a week earlier.) Nemerteans were collected as early as April 7 and as late as October 19. Although there were no nemerteans on the crabs collected between these two dates, from November through March, it is probable that if larger numbers of adult females had been available for examination worms would have been discovered on the gills. Only seven adult females were examined during that period.

To summarize the preceding discussion, the principal events in the life history of *C. c. imminuta* during the course of one year at Grand Isle are as follows: During the months of December, January, and February, when the host is not in berry, sexually immature worms remain on the gills of the adult female crab. Growth probably takes place during this period. Toward the end of March or early April, when the first batches of crab eggs are laid, the worms migrate from the gills to the egg masses, there becoming sexually mature. A few days after fertilization, the developing eggs are extruded from the body of the female worm, and hatching of the free-swimming larvae is completed within 11 days after fertilization. After the crab eggs hatch, the adult worms may return to the gills of the crabs. The free-swimming larvae have the following possibilities: (1) they may remain on the egg mass and develop into crawling worms there within a few days, migrating to the gills when the crab eggs hatch; (2) they may never come in contact with a host crab and as a result die; (3) they may be eaten by plankton feeders; (4) they may reach the gills of a male crab, develop only a short time, and then be cast off and die; (5) they may reach the gills of an immature female and soon be cast off with the exuvium; (6) they may reach the gills of an adult non-ovigerous female and remain there over winter until the crab becomes ovigerous the following spring, when the worms would migrate to the egg mass, become sexually mature, etc.; (7) they may reach the egg mass of a female, migrate to the gills when the crab eggs hatch, and remain there until another batch of crab eggs is laid.



TABLE 13.—DECAPOD CRUSTACEANS EXAMINED FOR *C. c. imminuta* AT GRAND ISLE, LA.  
(The letter "o" indicates the presence of orange egg masses, the letter "b" brown egg masses.)

Name of Crab	Number and Sex	<i>C. c. imminuta</i>
Natantia		
Caridea		
Crangonidae		
<i>Crangon heterochaelis</i> (Say).....	1 female	None
Reptantia		
Paguridea		
Paguridae		
<i>Clibanarius vittatus</i> (Bosc).....	10 females	None
Brachyura		
Oxystomata		
Calappidae		
<i>Calappa flammea</i> (Herbst).....	1 female	None
<i>Hepatus epheliticus</i> (Linnaeus)....	2 females	None
	1 female	1 on gill (0.74 by 0.26 mm)
Leucosiidae		
<i>Persephona punctata aquilonaris</i> Rathbun.....	1 female (b)	3 adults on eggs (1.11 by 0.20 mm 1.66 by 0.20 mm 1.48 by 0.18 mm)
	1 male	None
Brachygnatha		
Portunidae		
<i>Ovalipes ocellatus gadulpensis</i> (Saussure).....	1 female 2 males	None None
<i>Portunus sayi</i> (Gibbes).....	9 females 1 female 6 females (o) 3 females (b)	None 1 minute worm (lost) None None
<i>Callinectes ornatus</i> Ordway.....	1 female 1 female 1 female (b) 25 males	None 5 small worms on gills 1 worm on egg mass (1 mm in length) None
<i>Arenaeus cribrarius</i> (Lamarck)....	3 females 1 female 3 males	None 1 worm on egg mass (1.2 by 0.2 mm) None

TABLE 13.—Concluded

Name of Crab	Number and Sex	<i>C. c. imminuta</i>
Brachygnatha (concluded)		
Xanthidae		
<i>Panopeus herbstii</i> H. Milne-Edw...	4 females	None
	1 female (b)	3 worms, about 1.5 mm in length, and 2 empty sheaths, all on eggs
	3 males	None
<i>Eurypanopeus depressus</i> (Smith)...	1 female (b)	None
<i>Eurytium limosum</i> (Say).....	2 males	None
<i>Menippe mercenaria</i> (Say).....	1 female	None
	1 female (soft)	None
	4 females (o)	None
	1 female (b)	Several small worms and egg cords on egg mass
	1 female (b)	1 small worm on eggs
	1 male (soft)	None
	3 males	None
Grapsidae		
<i>Sesarma cinerea</i> (Bosc).....	2 females (b)	None
<i>Sesarma reticulatum</i> (Say).....	2 females	None
	1 male	None
Ocypodidae		
<i>Ocypode albicans</i> Bosc.....	1 female	None
	2 females (b)	None
<i>Uca minax</i> (Le Conte).....	2 females (b)	None
Inachidae		
<i>Libinia dubia</i> Milne-Edw.....	1 male	None

## GEOGRAPHICAL DISTRIBUTION AND HOSTS

During June and July, 1940, 108 decapod crustaceans other than *Callinectes sapidus*, almost all Brachyura, were examined for *Carcinonemertes*. These represented 18 species, and were collected within a radius of 15 miles of Grand Isle. The crustaceans examined and infestations recorded are shown in Table 13.

Seven species of Brachyura, in addition to *Callinectes sapidus* Rathbun, were found, as indicated in Table 13, infested with *Carcinonemertes carcinophila imminuta*. These are *Hepatus epheliticus* (Linnaeus), *Persephona punctata aquilonaris* Rathbun, *Portunus sayi* (Gibbes), *Calli-*

TABLE 14.—DISTRIBUTION RECORDS OF *C. c. imminuta*, BASED ON MUSEUM MATERIAL

Name of Host	Locality and Date	Length (mm)	Diameter (mm)	Basis ( $\mu$ )	Stylet ( $\mu$ )	S:B Ratio
<i>Portunus spinicarpus</i> (Stimpson), USNM 76946, 76909, 76939...	10 miles south of the Tortugas, Fla.	4.0 3.5	0.23 0.21	23.0 x 6.0 22.0 x 6.0	8.0 ...	0.347 .....
<i>Callinectes bocourti</i> Milne-Edwards, USNM 59281.....	Fox Bay, Colon, Panama	1.3	0.35	21.0 x 5.5	...	.....
<i>Callinectes bocourti</i> Milne-Edwards, USNM 24456.....	Catano, San Juan Harbor, Puerto Rico	only a fragment of a sheath				
<i>Callinectes marginalis</i> Milne-Edwards, MCZ 8864, USNM 7648..	St. Thomas, West Indies, 1871 and 1884	3.5	0.28	21.0 x 5.5	...	.....
<i>Callinectes danae</i> Smith, MCZ 5145.....	Rio de Janeiro, Brazil, 1865	... ... ... 6.0 12.0 3.0	0.14 0.15 0.15 0.26 0.21 0.15	21.7 x 6.0 19.5 x 6.0 21.0 x 6.0 20.0 x 6.0 21.0 x 5.5 18.0 x 5.5	7.0 8.5 ... ... ... ...	0.323 0.436 ..... ..... ..... .....
<i>Cronius ruber</i> (Lamarck), USNM 59292.....	Porto Bello, Panama, Atlantic side, 1912	2.0	0.16	20.0 x 5.5	7.0	0.350



*nectes ornatus* Ordway, *Arenaeus cribrarius* (Lamarck), *Panopeus herbstii* Milne-Edwards, and *Menippe mercenaria* (Say). The genera *Portunus*, *Callinectes*, and *Arenaeus* belong to the family Portunidae, *Hepatus* to the Calappidae, *Persephona* to the Leucosiidae, and *Panopeus* and *Menippe* to the Xanthidae.

The worms on all these hosts were extremely few in number and small in size, when compared with those found on *C. sapidus*, although all were identical specifically. Therefore the writer has come to the conclusion that *C. sapidus* is the normal host for *C. c. imminuta*, at least in the Grand Isle area, and that the seven other hosts are more or less accidentally infested. It will be pointed out later that the members of the genus *Carcinonemertes* are generally restricted in choice of hosts to members of the Portunidae.

At Grand Isle, the infestation of the non-portunid genera, *Hepatus*, *Persephona*, *Panopeus*, and *Menippe*, was probably brought about by the extremely favorable environment for the dispersal and transfer of the free-swimming larvae. *Callinectes sapidus* is abundant and highly infested with nemerteans. These other crabs come in close contact with *C. sapidus*, allowing the infestation to be carried over. The shallow water, lack of strong currents, great abundance of crabs, and the close association of the various species of crabs all contribute to the spreading of the infestation to species other than *C. sapidus*. The data suggest that there is no host specificity. The worms will evidently thrive on almost any of the littoral aquatic crabs, if given a chance to become established there.

In addition to those records marked with an asterisk in Table 3, which may be referable to the variety *imminuta*, other records were obtained from crabs in the collections of the Museum of Comparative Zoology and the United States National Museum. These are shown in Table 14. Measurements of the body and the stylet apparatus are included wherever possible.

All these worms conform to the description given above of the variety *imminuta*. The worms from *Callinectes danae*, however, appear to be slightly larger and to possess a larger posterior proboscis chamber. In the last three of these worms listed above the posterior proboscis chamber measured 183 by 56, 140 by 77, and 160 by 50  $\mu$  respectively, being about three times the size of the same structure in fixed and sectioned specimens of *C. c. imminuta* from Grand Isle. These very slight differences may have been caused by variations in method of killing and fixing. The worms from *C. danae* were all taken from one crab, but the method of killing is unknown. A study of live worms from Rio de Janeiro will be necessary before such variations as now seem to exist can be shown to be significant.

The "worms with lateral eye spots" found by Pearse (1932) on

*Bathynectes superba* (Costa) at 20 miles south of Tortugas, Florida, probably were the variety *imminuta*.

*C. c. imminuta* has been found in the Gulf of Mexico, the West Indies, including the Caribbean Sea, and as far south as Rio de Janeiro, Brazil.

### CARCINONEMERTES EPIALTI COE

THE FIRST nemertean living on crabs reported from the Pacific Ocean was *Carcinonemertes epialti* Coe (1902a). This species was found on a kelp crab, *Pugettia producta* (Randall), formerly *Epialtus productus* Randall, collected at Monterey, California. The original description was repeated by Coe in later works (1904b, pp. 150-154; 1905a, pp. 230-233). In the latter paper he showed (Pl. 2, fig. 20) a colored figure of the worm, the first ever published. In 1905(b) and 1940 Coe again mentioned this species but gave no additional information.

The distinctive specific characteristics are as follows: Sexually mature individuals about 4-6 mm in length; proboscis very minute and short, extending scarcely more than its own diameter posteriorly to the brain; basis 27-33  $\mu$  in length and 5-8  $\mu$  in diameter, often somewhat asymmetrical; stylet 12-15  $\mu$  in length; posterior proboscis chamber bent at angle to anterior part of proboscis in ordinary states of contraction. The remaining part of Coe's original description, from which this brief list of characters has been taken almost verbatim, is occupied mainly with a discussion of generic characteristics.

The writer examined three ovigerous specimens of *Pugettia producta* in the collection of the Museum of Comparative Zoology, no. 2125 from Crescent City and no. 314 from San Francisco, California, but found no nemerteans. However, 24 specimens of *Euphylax dovii* Stimpson, a portunid crab, nos. 8766, 8765, 5464, and 8868 in the Museum of Comparative Zoology, all from Payta, Peru, yielded five specimens of *Carcinonemertes epialti* Coe. No date of collection was attached to the specimens.

The measurements of these Peruvian specimens are shown in Table 15.

In all five Peruvian specimens the posterior end of the basis is slightly larger than the anterior end (fig. 28), agreeing with the description of the basis in the Californian worms. Although the angle at which the posterior chamber of the proboscis is turned is not acute, in each worm the chamber is bent upward slightly toward the dorsal body wall. The method of fixation may have altered the relative position of the posterior chamber. The cephalic glands in the Peruvian specimens are well developed and there are distinct muscle fibers in the head region, extending in various directions around the rhynchodaeum and the anterior part of

TABLE 15.—MEASUREMENTS OF *C. epialti* TAKEN FROM *Euphyllax dovii* AT PAYTA, PERU

Sex	Length (mm)	Diameter (mm)	Basis ( $\mu$ )	Stylet ( $\mu$ )	S:B Ratio	Middle Chamber ( $\mu$ )	Posterior Chamber ( $\mu$ )
Female.....	5.5	0.350	.. x 7	....	.....	42 x 34	91 x 67
Female.....	2.5	0.350	.. x 6	....	.....	30 x 23	56 x 45
Female.....	2.0	0.245	21 x 7	....	.....	25 x 19	50 x 45
Female.....	4.0	0.315	24 x 6	10.5	0.437	35 x 28	84 x 70
Immature.....	1.5	0.175	25 x 7	....	.....	28 x 23	42 x 35
Averages.....	3.1	0.287	23.3 x 6.6	10.5	0.437	32 x 25	65 x 52

the esophagus. Other anatomical features agree with the description of *C. epialti* given by Coe (1902a).

Although the basis in the Peruvian worms appears to be a little shorter than in the Californian specimens, such a difference probably is not significant, inasmuch as the size of this structure is known to vary somewhat individually and inasmuch as only a very few specimens were available for measurement. The ratio of stylet to basis in specimens from the two regions is nearly identical.

The mucous sheaths in which the Peruvian specimens were found resembled those of *C. c. imminuta*. The surface was covered with round or irregular lapilli, whitish in color, and of slightly different sizes (fig. 2), or with elongated, longitudinal raised areas (fig. 24). The sheaths were all a little longer than the worm in the contracted state.

## *CARCINONEMERTES MITSUKURII* TAKAKURA

### TRANSLATION OF ORIGINAL DESCRIPTION

THIS JAPANESE species has been mentioned only once in the literature, and that in the original description by Takakura (1910). Since the description was published in Japanese, it has remained inaccessible and unrecognized by students of the nemerteans, even though the paper contains the first mention of the unique male reproductive system. Therefore, the writer here presents the complete paper, with the exception of the figures, translated by Dr. Richard R. Kudo, Associate Professor of Zoology at the University of Illinois.

### ON A NEW SPECIES OF PARASITIC NEMERTEAN

The so-called parasitic nemerteans are mostly either symbiotic or temporarily attached to the outside, or live inside, of other animals. There are only three truly parasitic species, in two genera. These are *Carcinonemertes carcinophila* (Kölliker)



found in the North Atlantic and Mediterranean Sea, *Carcinonemertes epialti* Coe found on the Pacific coast of North America, both on crabs, and *Cephalothrix galathea* Dieck found in Sicily on *Galathea strigosa* Linnaeus. The species under discussion was first found in Yokohama harbor in July, 1895, by Professor Mitsukuri. It belongs to the genus *Carcinonemertes*. At that time the harbor breakwaters were under construction and the concrete wall had cracked in places. The port authorities raised the sunken and cracked concrete blocks for examination. At that time Professor Mitsukuri collected several specimens of *Lineus* from the raised material, and he kindly advised me that further examination of the material might bring out valuable information concerning these worms. Therefore I went to the same locality to examine the concrete blocks brought up. In addition to *Lineus*, I found a very small crab that had an egg mass in which I found only two very small specimens of *Carcinonemertes*, a male and a female. So I waited for the opportunity to collect more material. I examined many crabs, particularly their egg masses. Finally in April, 1906, at the mouth of the Minato River, which flows into Tateyama Bay, I collected "moku gani" (small crabs, *Eriocheir japonicus* de Haan), one of which had an egg mass in which I found several dozen worms.

The body is cylindrical, filiform, with the extremities bluntly pointed and about the same in shape. There are two black eye spots located slightly back of the anterior end. The color is light brown, light yellow, or milky white. The brain in life can be seen through the tissue as a small, fleshy mass. Males and females vary in length. The extended males are only 1 cm, while extended females are three times or more as long. The maximum width for both sexes is 0.5 mm. The body secretes mucus which forms a semi-transparent tube by which the animals are attached to the bristles on the swimmerets of the host. If removed from the tube and put in sea water in a watch glass, the worm secretes mucus and attaches itself securely to the glass. Apparently this mucus is necessary to prevent the worm's being washed away by the currents.

The integument is thick, and directly below it is a thin basement membrane. There is a thin circular and a relatively thick longitudinal muscle layer, agreeing with those in other *Metanemertini*. Internal to the longitudinal muscles are well developed hypodermal glands, distributed over the body length, though between the longitudinal muscles and the digestive tube they become narrowed. Near the posterior end of the body these glands form a thick layer. Near the anterior end, the glands surround the rhynchodaeum and are grouped to form the cephalic glands. These open on the dorsal side of the head adjacent to the rhynchodaeum pore. The posterior part of the cephalic glands extends posteriorly to the brain. The function of these glands, both hypodermal and cephalic, probably concerns the production of mucus. In other parasitic worms similar glands produce mucus.

The digestive tract is roughly like that of other *Metanemertini*. The anterior end of the esophagus joins the rhynchodaeum just anteriorly to the brain. The esophagus is short and narrow, enlarged behind the brain and developing folds. Here it becomes the cardiac part of the stomach. The pyloric part follows; it has no folds. It is a narrow, elongated tube longer than the cardiac part in most species, but in this species it is very short and inconspicuous. The intestine has very wide caeca. These develop ventrally from the junction of the stomach and intestine and all around the stomach. A pair of caeca develop from the dorsal side of the stomach and reach near the brain. Along the sides of the intestine there are deep, blind sacs, which are not so deep near the posterior end.

The rhynchodaeum, i.e., from the point where the proboscis is attached to the anterior end of the head, is a narrow tube in common with the esophagus. The rhynchodaeum and proboscis are both short and extend only to the middle of the stomach. The part surrounding the rhynchodaeum is imperfect, with only thin connective tissue and without muscle layers.

The proboscis is short and thick, filling the rhynchocoel. There is no space between it and the wall. The proboscis sac is divided into three chambers. The anterior proboscis chamber has a stylet apparatus and is very short and narrow,

with no glands, although in most species of nemerteans it is long and glandular. The posterior part of this chamber, bearing the stylet, has very stout glandular walls. The stylet is small, measuring  $8\ \mu$  in length. The elongated, oval basis reaches  $27\ \mu$  in length. Secondary stylets and secondary stylet sacs are absent. The middle chamber has a muscular wall and large lumen. The posterior chamber is short but wide and ovoid, and glandular epithelium covers the inner surface. The anterior and posterior chambers are of different shapes, but both are short and wide. The posterior end of the hind chamber is close to the rhynchocoel wall and no muscles are attached as in other species. In *C. epialti* the posterior chamber is bent upward but in this species it is close to the ventral side.

There is a pair of lateral blood vessels, connected at the anterior and posterior ends. There is no dorsal blood vessel. The point of union at the anterior end is far posterior, as compared with ordinary species, being located immediately in front of the brain.

The excretory system as in other species of the genus is absent.

The brain is of the usual form, with right and left parts and dorsal and ventral regions. The lateral nerve cords are considerably swollen toward the posterior end of the body. The posterior commissure is on the ventral side of the posterior end of the intestine.

The reproductive organs begin behind the stomach and reach the posterior tip of the body. The testes are numerous and occur in the vicinity of the intestine. In one section there may be seen sometimes 30 testes arranged in 1 to 3 rows. Even when the reproductive elements (spermatozoa) are mature no external pores are seen. On the other hand the ovaries are arranged regularly between the caeca of the intestine on the right and left. The pores of the oviducts are located on the dorsal side of the body near the median line.

The most striking characteristic of this species is the presence of a dorsal duct running along the mid-dorsal line. It looks like a dorsal vessel but is not. The character of its wall and the relation to other organs is different.

It arises immediately behind the rhynchocoelom. Its course is similar to that of the dorsal vessel. It is a narrow tube found only in males, never in females, and reaches to the posterior end of the body. Ordinarily it is slightly larger than the lateral blood vessel, but at places it becomes very much enlarged. The posterior end obviously connects with the digestive tube immediately in front of the anal opening. The wall of the dorsal duct is a layer of squamous cells, each possessing a conspicuous nucleus, just as in excretory tubes, but never made of pavement cells as in the blood vessels. Near its posterior end there is a circular (sphincter) muscle. In the lumen of the dorsal duct there are always to be found mature sperm cells, and, moreover, the spermatozoa have been seen moving from the testes into the dorsal duct. Furthermore, even in mature testes there is no trace of direct communication to the outside through an external pore, and the dorsal duct has been found only in males. Therefore, I think that the dorsal duct is a unique sperm duct in this particular species. It is entirely new, being unknown among the hitherto known nemerteans. The presence of spermatozoa in the dorsal duct, which I mentioned previously, may be due to the contraction of the body of the worm, in which the testes had become broken and their contents thrown into the dorsal duct. But that such a special duct is present in connection with the digestive tube is certainly noteworthy. With what organs of other species this dorsal duct is homologous is not clear, because I have not studied the development of the worm, but, based upon anatomical observation, there might be some relation between the presence of the dorsal duct and the shortness of the proboscis sac. The proboscis sac in the male has a very small posterior chamber, and behind that it becomes a bundle of fibers directed slightly dorsally and reaching the inner surface of the longitudinal muscle layer. Then gradually little spaces develop in that bundle of fibers, and further along it is clearly surrounded by a cellular wall, thus becoming the dorsal duct. In the female it is the same as far as the point where the structure comes in contact with the longitudinal muscle layer, but then

there is no recognizable structure beyond that point. Therefore the so-called dorsal duct mentioned here is the proboscis sac, which has been suddenly pinched off behind the proboscis. Thus there are two parts to the proboscis, anterior and posterior. In the males the anterior region is short and a true proboscis sac, while the posterior part becomes finally connected with the posterior end of the intestine. Thus it serves as a sperm duct in this sex, while in the female the posterior part has degenerated completely.

There is no sensory cerebral organ.

From what is known about the two species of this genus the young worms are attached to the gills of the host and suck its blood. When they become mature they enter the egg mass and there become sexually ripe and deposit their eggs in mucous tubes. After segmentation the larvae develop, leave the egg shell, and stay among the crab eggs or inside the tube. As the worms develop they molt and assume the usual form, creeping on the body surface of the host and reaching its gills, where they live until the next year. Therefore the worms found on the egg masses are always without exception mature.

The specimens I collected were all mature ones, because none were found on the gills. This Japanese species probably has the same life cycle as foreign species, but on this I cannot be positive. The host crab, *Eriocheir japonicus*, lives only in fresh or brackish water. At the time of this collection (1906) there was a heavy rainfall and flood, which carried the crabs down to the bay into brackish water. I never found the worms again, although I searched repeatedly. The crab lives in Yokohama Bay, where the salt concentration is high, as well as in fresher waters. I became curious whether the fresh water crabs are parasitized with this nemertean but unfortunately none were collected up to the present time.

Comparison of the new species with the known species: (1) the lateral nerve trunk goes around the ventral side of the posterior end of the intestine, instead of around the dorsal side as in other species; (2) the anterior commissure of the lateral blood vessels is located far behind the usual point; (3) a special dorsal vessel, present in males only, is entirely different from other species.

Therefore I propose to name this species *mitsukurii*, not only in honor, but in commemoration of Professor Mitsukuri.

#### GEOGRAPHICAL DISTRIBUTION AND HOSTS

Many specimens of nemerteans which the writer believes should be, for the time being at least, referred to as *Carcinonemertes mitsukurii* Takakura were collected from the egg masses of several crabs in the collections of the Museum of Comparative Zoology and the United States National Museum. These are shown in Table 16. A few measurements of those specimens which were cut in such planes as to facilitate accurate measurement are included.

All the crab hosts shown in Table 16 belong to the Portunidae. In most respects the worms agree with Takakura's description. The basis, however, is slightly shorter. The writer is unable to state whether this difference is significant. It may be that the basis in this species is variable in size over a range wide enough to include the above measurements. It is impossible to determine from the sectioned material whether the anal commissure of the lateral nerves passes above or below the posterior end of the intestine. The posterior proboscis chamber in all these worms is short and thick, and about twice as long as wide, corresponding to



TABLE 16.—DISTRIBUTION RECORDS OF *Carcinonemertes mitsukurii* BASED ON MUSEUM MATERIAL

Name of Host	Locality and Date	Length (mm)	Diameter (mm)	Basis ( $\mu$ )	Stylet ( $\mu$ )
<i>Charybdis miles</i> de Haan USNM 50792.....	San Andreas I., between Ma- rinduque and Luzon, P. I., 1908	2.2 2.7	0.13 0.14	22.5 x 7.0 .....	... ...
<i>Charybdis cruciata</i> USNM 2112 (Herbst)...	Hong Kong, China	3.5	0.28	20.5 x 7.0	...
<i>Charybdis erythrodactyla</i> MCZ 5337 (Lamarck)...	Kauai, Hawai- ian Is.	badly disintegrated			
<i>Charybdis erythrodactyla</i> MCZ 636 (Lamarck)....	Apiang, Kings- mills Is., 1860	5.5	0.24	20.5 x 5.0	...
<i>Charybdis erythrodactyla</i> MCZ 5339 (Lamarck)...	Society Islands	16.0 1.4	0.60 0.11	..... 21.0 x 8.0	... ...
<i>Charybdis erythrodactyla</i> USNM 29654 (Lamarck)	Honolulu market	5.6 5.0	0.31 0.22	21.0 x 6.5 22.5 x 7.0	8.5 .
<i>Portunus pelagicus</i> MCZ 1638 (Linnaeus)...	Singapore	badly disintegrated			

*mitsukurii*. There are cephalic muscle fibers around the rhynchodaeum (fig. 9), as in other species of the genus. The shape of the basis is shown in fig. 29. Sketches of the mucous sheaths of this species are found in figs. 1, 3, and 41.

A comparison of the three points which Takakura considered diagnostic characters for his species with the situation found in *C. c. imminuta* and other species in the genus will show that all three of the items can no longer be held diagnostic of *mitsukurii* alone. The anal nerve commissure is ventral in both *imminuta* and *mitsukurii*, the anterior blood vessel commissure in both is located immediately in front of the brain, and in both species there is found the unique type of male reproductive system, referred to by the writer as Takakura's duct. One clear difference between the two species seems to be the fact that in *mitsukurii* the anal blood vessel commissure crosses dorsally to the posterior end of the intestine, while in *imminuta* it crosses ventrally to it. As for other diagnostic features of *mitsukurii*, little can be stated with certainty. Accord-

ing to Takakura (1910), there is a pair of caeca from the dorsal side of the stomach reaching near the brain. It must remain for future investigations, involving the comparative study of live and properly fixed material from various regions, to decide whether *C. mitsukurii* shall stand as a distinct species or shall be placed in synonymy with *C. carcinophila*. In the meantime the writer feels that it is best to consider all these worms from the western and central Pacific Ocean as belonging to *C. mitsukurii*. Such a treatment may avoid taxonomic confusion later on.

*CARCINONEMERTES COEI* SP. NOV.

SIX SPECIMENS of a hitherto unknown nemertean belonging to the genus *Carcinonemertes* were found on the egg mass of a single female specimen of *Charybdis natator* (Herbst), no. 5341 in the collection of the Museum of Comparative Zoology at Cambridge, Massachusetts. The crab, which belongs to the family Portunidae, had been collected at Zanzibar, on the east coast of Africa, in 1862. One of the worms sectioned very unsatisfactorily. The other five specimens, two males and three females, were successfully cut into serial sections 10  $\mu$  thick. Considerable difficulties were encountered because of the mucous sheaths surrounding the worms and because of the poor fixation (probably in 70 to 80 per cent alcohol). Four of the serial sections were stained with safranin and fast green. The fifth was stained with Heidenhain's iron haematoxylin. All the worms were in separate sheaths, except two, a male and a female, which were in the same sheath.

Although, like the other species of the genus, the characteristics by which this species can be distinguished from related species are small, nevertheless there are a few fundamental differences between each of the known species and the new worm. The writer proposes to name the new species *Carcinonemertes coei*, in honor of Dr. W. R. Coe. The diagnosis of the species is as follows:

*Carcinonemertes coei* sp. nov.

Genus *Carcinonemertes*. Body stout (fig. 23), with both ends rounded, and of about the same diameter throughout. Average length 6 mm, average diameter 0.5 mm, about 10 times longer than wide in preserved specimens. Head not demarcated from body. No lateral grooves or cerebral sense organs.

Mucous sheath (fig. 35) several millimeters longer than body. Lapilli on surface of sheath small, about 140 by 90  $\mu$ , light brown in color and widely scattered. Lapilli not all of same shape, but some elongated and poorly delimited.

Color in preserved specimens yellowish white. Single pair of ocelli, slightly irregular in shape, very dark brown or black, about 27  $\mu$  in

diameter, located  $160\ \mu$  apart at a level  $145\ \mu$  behind the anterior tip of the body (fig. 35).

\* Proboscis much reduced in size. Anterior chamber thin-walled and narrow. Basis (fig. 4)  $22.7\ \mu$  in length, swollen posteriorly. Posterior diameter  $7.5\ \mu$ , anterior diameter  $3.7\ \mu$ , posterior end being twice as large as anterior end. Basis stains heavily with safranin and with Heidenhain's iron haematoxylin, as in other species. Basis surrounded at least in its posterior two-thirds by a single layer of cells. Stylet (fig. 4) slender,  $8.7\ \mu$  long, or about  $\frac{1}{3}$  to  $\frac{1}{2}$  as long as the basis. Ratio of stylet to basis 0.382. Gland cells associated with stylet apparatus bunched posteriorly, near posterior end of basis. Middle proboscis chamber highly muscular, fibers running in various directions. Size of middle chamber 33 by  $28\ \mu$ , slightly longer than its diameter, situated posteriorly to basis with its anterior half enclosed by the enlarged glandular tissue associated with the basis and stylet. Posterior chamber of proboscis non-muscular, glandular, thick-walled, situated immediately posteriorly to the middle chamber and in approximately the same plane as the preceding part of the proboscis. Size 78 by  $47\ \mu$ , longer than wide.

Esophagus large and muscular as in other species of genus. Alimentary canal straight and presenting few peculiarities, other than the reduction in size of the lateral pouches because of the enormous development of the ovaries.

Nervous system as in other species of genus.

Cephalic glands, submuscular glands, outer epithelium, circular and longitudinal muscle layers, and cephalic muscle fibers similar to those in other species.

Testes numerous, scattered through the region between submuscular glands and intestine. Takakura's duct present.

Ovaries very numerous. In sections an inner and an outer row on each side of the intestine (fig. 33), making four rows in all. Outer row situated close to submuscular glands, inner row located deeper in the body adjacent to the intestine. Ovaries in the two rows alternate with some, but not absolute, regularity. Each ovary with several developing eggs. Intestinal pouches apparently much reduced in size, the space between the submuscular glands and the intestine being almost wholly occupied by the ovaries. (Fixation was so poor that it was virtually impossible to distinguish the intestinal pouches.) In sections, three-fourths of the diameter of the body is made up of ovaries, which extend from the anterior end of the intestine to the posterior end of the body.

This species differs from known species in having a much stouter body (compare figs. 22 and 23), the basis being swollen posteriorly (compare fig. 4 with figs. 27, 28, 29, 30, and 31), and there being two rows of ovaries on either side of the intestine (compare figs. 26 and 33).

At present *Carcinonemertes coei* is known only from the egg mass



TABLE 17.—MEASUREMENTS OF *Carcinonemertes coei* SP. NOV.

Sex	Length (mm)	Diameter (mm)	Length of Basis ( $\mu$ )	Diameter of Basis ( $\mu$ )	Stylet Length ( $\mu$ )	S:B Ratio	Middle Chamber ( $\mu$ )	Posterior Chamber ( $\mu$ )
Male.....	4.2	0.5	...	8.4-4.2	..	.....	30 x 20	63 x 28
Female.....	5.8	0.6	...	6.3-4.2	..	.....	35 x 31	84 x 68
Female.....	6.0	0.7	21	6.0-2.5	8	0.381	38 x 31	108 x 70
Female.....	8.0	0.4	24	8.4-3.5	9	0.375	25 x 38	62 x 35
Male.....	...	...	23	7.5-4.0	9	0.391	35 x 19	73 x 35
Averages...	6.0	0.5	22.7	7.5-3.7	8.7	0.382	33 x 28	78 x 47

of a single specimen of *Charybdis natator* (Herbst) mentioned above. The holotype and four paratypes have been deposited in the Museum of Comparative Zoology at Cambridge, Massachusetts.

Table 17 shows the individual measurements of the five specimens upon which the preceding description is based.

## THE FAMILY ASSIGNMENT OF THE GENUS

### THE GENERA OF THE EMPECTONEMATIDAE

THE HOPLONEMERTEAN suborder Monostilifera was divided by Böhmig (1933) into two tribes, the Archimonostilifera, in which the mouth and proboscis open separately, and the Eumonostilifera, in which the mouth and proboscis have a common opening. To the latter tribe belongs the family Empectonematidae Bürger (1904), in which the genus *Carcinonemertes* has been placed by most modern writers. Böhmig (1933) characterized the family as having long, flat, thread-like bodies, short and relatively thick proboscides, very much reduced or absent cerebral organs which lie in front of the brain, few eyes (often 4, 2, or 0), and being of separate sexes.

Five genera were listed by Böhmig (1933) in this family, but since that time five other genera have been described which in the writer's opinion belong in or near this family. The ten genera are as follows:

Emplectonema (Stimson, 1857, p. 163)	Arenonemertes (Friedrich, 1933, p. 504)
Paranemertes (Coe, 1901, p. 32)	Nemertellina (Friedrich, 1935, p. 10)
Nemertopsis (Bürger, 1895, p. 548)	Nemertellopsis (Friedrich, 1935, p. 12)
Gononemertes (Bergendal, 1900, pp. 313-328)	Atyponemertes (Friedrich, 1938, p. 22)
Carcinonemertes (Coe, 1902b, pp. 409-411)	Dichonemertes (Coe, 1938, p. 221)

The two genera *Gononemertes* and *Carcinonemertes* appear to be more closely related to each other than to the rest of the genera. *Gonone-*

mertes has no stylet apparatus and *Carcinonemertes* has only one central stylet. The other genera have the central stylet and in addition one or two pairs of accessory stylet pouches.

#### DIAGNOSIS OF THE *CARCINONEMERTIDAE*

The first and only use of the name *Carcinonemertidae*, in so far as the writer is aware, is that of Sumner, Osburn, and Cole (1913). In their list of the fauna of Woods Hole and vicinity (p. 591), they listed *Carcinonemertes carcinophila* (Kölliker) as follows:

#### FAMILY *CARCINONEMERTIDAE*

*Carcinonemertes carcinophila* (Kölliker)

Coe, 1902, 441.

Nobska Point, Katama Bay, Nememsha Bight.

"Parasitic on the gills of various species of crabs when young, migrating to the egg masses of the crab at the approach of sexual maturity." Locally reported only from the "lady crab" (*Ovalipes ocellatus*). In the case of a large number of crabs of this species examined by Dr. Coe during July and August of various years the parasites were found on the gills of about 10 per cent of the female crabs, but none were found on the males.

No diagnosis or description of the new family *Carcinonemertidae* was given, nor was the name *Carcinonemertidae* designated as a new family name. No indication of the genera and species to be included in the family was given, other than the mention of *C. carcinophila*.

There is nothing in the International Rules of Zoological Nomenclature which governs the proposing of new family names, except that they must end in -idae, must be founded upon the type genus, and must be uninomial. The name *Carcinonemertidae*, therefore, is a valid name.

A brief diagnosis of the family *Carcinonemertidae* (Sumner, Osburn, and Cole, 1913) is as follows:

Monostiliferan hoplonemerteans living as ectohabitants on the gills and egg masses of crabs. One central stylet, no accessory stylet pouches or accessory stylets. Proboscis very short, reaching scarcely beyond the posterior end of the muscular part of the esophagus. Anterior chamber of the proboscis extremely short and non-glandular. Lateral nerves lie internal to the massively developed submuscular glands. Cephalic glands well developed. No cerebral sense organs. Cephalic muscle fibers present. Excretory apparatus apparently absent. Dorsal blood vessel absent. Takakura's duct present in males. Internal fertilization and viviparity commonly occur. Excessive development of eggs and spermatozoa. Mucous sheaths secreted, attached to abdominal endopodite hairs of ovigerous crabs.

The family includes one genus, *Carcinonemertes*, with four species, *C. carcinophila carcinophila* (Kölliker), *C. carcinophila imminuta* described above, *C. epialti* Coe, *C. mitsukurii* Takakura, and *C. coei* also described above.

The family Carcinonemertidae may be distinguished from the most closely related family, the Emplectonematidae, by the following characteristics: (1) members live as ectohabitants of crabs; (2) one central stylet, no traces of accessory pouches or stylets; (3) no cerebral organ; (4) Takakura's duct in males; (5) massive development of both cephalic and submuscular glands.

The adoption of the family Carcinonemertidae leaves the other nine genera in the family Emplectonematidae. Of these Gononemertes is outstanding and probably will not remain in that group when more is known about its anatomy and development.

As Coe (1902a) has stated, the members of the genus Carcinonemertes appear to be more modified in relation to their dependent way of life than Gononemertes, although they still retain ocelli and a central stylet in the proboscis.

### KEY TO SPECIES

IT SHOULD be apparent that the use of a key alone for identification of an unknown worm in this genus would be unwise. The investigator should have the most detailed descriptions at hand, together with not only one but if possible several specimens of the unknown worm, preferably of both sexes. Measurements made while the animals are alive are of great help in identification. The following key may serve as a preliminary aid in identification of species of the genus Carcinonemertes.

1. Ovaries in two rows on each side of the intestine, an inner and an outer row; basis twice as large in diameter posteriorly.....*C. coei*  
Ovaries in a single row on each side of intestine; basis nearly cylindrical....2
2. Posterior proboscis chamber bent dorsally at an angle to the proboscis; body less than 6 mm long.....*C. epialti*  
Posterior proboscis chamber not bent at an angle but in same plane as preceding part of proboscis; body may be less than 6 mm long, but usually more, reaching up to 70 mm.....3
3. Anal blood vessel commissure dorsal to posterior end of intestine..*C. mitsukurii*  
Anal blood vessel commissure ventral to posterior end of intestine.....4
4. Basis may be as short as 19  $\mu$ , usually from 25 to 30  $\mu$  in length, diameter 6 to 8  $\mu$ ; stylet 8 to 12  $\mu$  in length; body 20 to 70 mm in length.....*C. c. carcinophila*  
Basis ranges in length from 19 to 23  $\mu$ , averaging 21  $\mu$ , diameter 4.5 to 6  $\mu$ ; stylet 6 to 9.5  $\mu$ , averaging 7.4  $\mu$ ; body 0.4 to 35 mm in length, averaging about 10 to 25 mm.....*C. c. imminuta*

### SIGNIFICANCE OF TAKAKURA'S DUCT

THE REPRODUCTIVE system in the Nemertea is very simple in structure. The gonads in both sexes are usually placed alternately with the intestinal pouches. In some genera, however, i.e., Carcinonemertes males, Gonone-



mertes, Tubulanus, and Malacobdella, they are extraordinarily numerous and do not alternate regularly with the pouches of the gut.

Each gonad empties to the outside through an individual duct. In the case of *Zygeupolia*, described in detail by Thompson (1901, p. 713), the testis is a simple sac, with a single duct, opening on the dorsal surface of the body near the side of the rhynchocoel. The duct passes through the longitudinal and circular muscle layers, expands into a small bulb, and then opens to the exterior through the integumental epithelium. The ovaries do not have preformed ducts; the eggs are discharged by the rupture of the body wall.

Böhmig (1933, p. 53) stated, regarding the gonads of the Nemertea, that "ihre einfachen Ausführgänge münden zumeist auf dem Rücken oder an den Seitenflächen in einer oder in mehreren Reihen angeordnet nach aussen, seltener sind sie gegen die ventrale Körperfläche verschoben."

In some of the pelagic nemerteans, especially *Nectonemertes* and *Phallonomertes*, Coe (1926) described testes which in some respects remind one of the condition described above in *Carcinonemertes*. Each testis, located in the cephalic region, is retort-shaped, with its neck pointed ventrally and laterally. The body of the retort contains the germinal cells. The neck is marked off from the body of the gonad by a constriction, distal to which the neck then expands into a spacious chamber, whose wall is non-germinal and is provided with a few longitudinal muscle fibers. In this chamber (the seminal vesicle) the ripe spermatozoa collect prior to being discharged through a short sperm duct to the opening on the genital papilla. The opening of the seminal vesicle to the exterior appears to remain closed except when the bundles of spermatozoa are discharged.

The gonad is not always a simple sac. Friedrich (1939, p. 238) has described in *Amphiporella baltica* Friedrich a double-sacked gonad, with ventral and dorsal parts, opening in a common pore laterally. The same condition is present also in *Amphiporus bürgeri* Isler, according to Friedrich.

Secondary sexual characters are present only in members of the Polystilifera pelagica, all of which are pelagic nemerteans. In *Nectonemertes*, *Balaenanemertes*, and *Parabalaenanemertes* the testes open to the exterior on small papillae. In *Phallonomertes murrayi* Brinkmann the papillae are extended as slender penes, which, according to Brinkmann (1917, pp. 62-63), may be inserted into the oviducts of the female where their tips, stuffed with spermatozoa by the contraction of the musculature of the spermary, may break off. The genital papilla may thus serve as a spermatophore.

In so far as the writer is aware, no important variations from the typical sac-like testes with their single ducts to the exterior, other than those just mentioned, have been discovered in the phylum Nemertea. The translation of Takakura's work on *C. mitsukurii*, together with the writer's independent observations on *C. c. imminuta* and other species, brings to light a hitherto generally unrecognized type of male reproductive system in the males of Carcinonemertes. This has been referred to above as Takakura's duct.

The Nemertea have been derived phylogenetically by Reisinger (1933, p. 33) from the Acoela. Schepotieff (1912), using emulsions of *Cerebratulus lacteus* (a nemertean), *Prostherceraeus* (a turbellarian), and *Capitella* (an annelid), found that the Wassermann's reaction is positive between Nemertea and Turbellaria and negative between Nemertea and Annelida, indicating that the Nemertea are more closely related to the Turbellaria than to the Annelida. Bürger (1897-1907, p. 472) concluded also that the Nemertea probably arose from an ancestral stock of the Turbellaria, probably possessing simple reproductive organs. In the evolution of the modern Turbellaria the reproductive system has undergone many complications, while in the Nemertea it has remained very simple. The presence of Takakura's duct indicates that the male system is not always as simple as Bürger believed, however.

Bürger (1897-1907) derived from the Protonemertini (Palaeonemertea) two main lines, the Heteronemertini (Heteronemertea) and the Mesonemertini (Palaeonemertea in part). From the Mesonemertini he derived the Metanemertini (Hoploneurertea). The genus *Emplectonema* was placed as the most primitive of the Hoplonemertea and gave rise to the genus Carcinonemertes.

It is impossible to determine whether Takakura's duct is a structure carried over from some acoelan ancestor or whether it is a new structure. The duct somewhat resembles one of the paired male genital ducts found in the Acoela (von Graff, 1908, pp. 1950-1953, Pl. I, fig. 10, Pl. II, fig. 2). These ducts in the Acoela are paired and empty into a single median chamber provided with copulatory apparatus. The male genital opening is not associated with the alimentary canal. Since the primitive nemerteans have simple sac-like gonads with short, individual ducts leading directly to the exterior, and since Carcinonemertes is a rather advanced genus, being armed with a stylet and having nerves located well inside all the muscle layers of the body wall, it seems best to the writer to consider the condition of the male reproductive system in Carcinonemertes as a separate development, independent of possible acoelan ancestry. The hypothesis will be tested when the embryology of Takakura's duct is known. It is interesting to note that such an arrange-

ment, whereby the sperm duct empties into the alimentary canal, in reality forming a cloaca, is elsewhere present only in the Nemathelminthes and Tardigrada, unless the vitello-intestinal canal of some Trematoda be included.

## RELATIONSHIPS TO HOST CRABS

NEARLY ALL the worms at Grand Isle taken from brown egg masses contained, as mentioned above, dark brown or black particles in their intestines (fig. 47). These resembled roughly the eyes and chromatophores of the crab embryos in their size, shape, and color. Such particles were not found in worms taken from yellow or orange egg masses, in which the crab embryos had not yet developed pigmented eyes or chromatophores, nor were they found in worms from the gills. It has already been stated that the nemerteans are able to evert the posterior muscular part of the esophagus. Its movements when thrust out of the body consist of strong peristaltic contractions, originating anteriorly. The diameters of the esophagi of 10 adult worms averaged  $97\ \mu$ , with a maximum of  $170\ \mu$  and a minimum of  $41\ \mu$ . The eggs of *Callinectes sapidus* measure approximately  $245\ \mu$  in diameter. It thus seems impossible that the esophagus can surround the eggs. But by constant sucking and pressing motions of the esophagus the worm may be able to rupture eventually the egg membranes and draw out the soft parts of the embryonic crab within.

In a serial section of *C. c. imminuta* from *Callinectes marginatus* (Milne-Edw.) collected at St. Thomas, West Indies, in 1871, the writer has seen in the intestine many dark particles similar to those mentioned above in *C. c. imminuta* from Grand Isle. Of more significance, however, is the fact that several setae and the delicate chitinous covering of the prezoa can be seen, indicating that the worms are capable of feeding upon the crab embryos.

Van Beneden (1876) believed that the European *C. carcinophila* fed upon dead or disintegrating embryos of the crab host. But because of the rarity of such eggs and the great abundance of worms on any one egg mass it seems more probable that the nemerteans feed upon the living crab embryos also. Churchill (1919, p. 97) estimated that in an egg mass of the usual size there are from 1,700,000 to 2,000,000 eggs. The number of eggs eaten by the nemerteans even in extremely heavy infestations would probably be negligible.

It has been indicated above that growth apparently occurs while the worms are on the gills of the crab. The nature of the food necessary for such growth and the mechanism of obtaining it are uncertain. Coe



(1902a) suggested that the worms are able to evert the proboscis and puncture the gills with the stylet, thereafter drawing in blood from the wound by pumping motions of the esophagus. However, the writer has found no evidence for the eversion of the proboscis. The blood corpuscles of *C. sapidus*, figured by Howell (1886, Pl. XVII, figs. 6-8), are of sufficiently small size to be taken in by the nemerteans. The question whether the worms puncture the gills and feed upon the blood of the crab must remain unsettled until the actual process is observed, or until the worms can be made to ingest colored substances injected into the crab's blood which will not pass through the chitinous gill covering of their own accord. No injuries to the gills made by the nemerteans were seen by the writer.

If the worms feed only upon the eggs of the crabs then there is a long period of time between the times when the crab is ovigerous when the nemerteans go without food. The worms are sexually mature only on the egg masses, where food is abundant. When on the gills, the gonads are undeveloped or rudimentary. In starvation experiments with various turbellarians it has been observed that the reproductive organs are the first to disappear. Perhaps a similar situation exists in *Carcinonemertes*.

The writer was able to maintain specimens of *Carcinonemertes* from the gills of a crab alive in a finger bowl of clean sea water, changed once every day, for over two months. No observable modifications in internal structure were present at the end of that time. A similar ability to withstand separation from the normal host and food has been found by Riches (1893-1895, p. 22) in the commensal genus *Malacobdella*. *Carcinonemertes* is probably able to last over the winter months between the ovigerous states of the crab host without food. The worms coil up in their cyst-like capsules between the gill lamellae and remain quiescent. The water during the winter months is cooler, with the crabs migrating to greater depths, and the worms do not require as much food as in the summer months when the crabs frequent the warmer and more shallow waters.

No injuries to the gills, even in heavy infestations, were found, but a heavy infestation is, however, probably detrimental because the free flow of water between many of the lamellae is prevented. By a modification of the method of Damant (1920) the area of an average sized gill lamella was found to be about 56.8 square millimeters on each side of the median raphe. Three nemertean capsules were present on one side of the lamella, which measured in area 6.28, 7.80, and 4.11 square millimeters respectively, or a total capsule area of 18.19 square millimeters. Thus nearly one-third of the area of one side of the lamella was occupied by the worm capsules and obstructed from the free flow of water. In heavy infestations nemerteans are present between approximately every second

gill lamella, and the amount of interference with flow of water becomes considerable. From all appearances, however, the heavily infested crabs are just as vigorous as the uninfested ones. An attempt was made to determine experimentally the effects of the nemerteans, using a modification of the method employed by Keys (1928) with fish parasitized by isopods, in which the effect of the parasites was measured by their influence upon the death rate in various semilethal environments. However, the inadequate laboratory equipment at hand was not capable of producing trustworthy results. Hay and Shore (1918) have suggested that when the gill chambers become heavily infested with the barnacle *Octolasmis mülleri* the crab is doubtless weakened and made an easy victim for fish or storms.

Dieck (1874) in describing his *Cephalothrix galathea* (? = *C. carcinophila*) wrote:

Ist der Eiervorrath verzehrt, so ziehen sich die Thiere in die Kiemenhöhle des Krebses zurück, um da wahrscheinlich ihren Ectoparasitismus in veränderter Art fortzusetzen, indem sie die zarte Membran der Kiemen anbohren und so zum Blute des Thieres gelangen. Wenigstens fand ich nicht nur häufig die Kiemenhöhlen von Würmern bewohnt, sondern sah, auch beim Zerzupfen derselben aus dem Innern Blutzellen ausströmen, welche sich in nichts von denen der Galathea unterschieden und wahrscheinlich, weil kurz vorher verschluckt, noch unverdaut geblieben waren.

From the existing evidence the writer takes the view that the members of the genus *Carcinonemertes* are not true parasites but ectohabitants, which feed upon the eggs of the crab.

#### MODIFICATIONS COINCIDENT WITH ECTOHABITATION

IN THE members of the genus *Carcinonemertes* there is excessive development of the cephalic and submuscular glands. By means of the abundant mucus the worms are enabled to adhere to the body of the host. With the mucus they form their capsule walls when living on the gills and their tough, elastic sheaths while on the egg masses.

Complicated sense organs on the head, such as are present in many nemerteans, are absent in these worms which live a sheltered life on the body of the crab.

The posterior part of the esophagus is modified into a large, muscular chamber which by its peristaltic pumping action draws food into the body.

The proboscis is very much reduced and immobile. The chief functions of the proboscis in other nemerteans are food-getting and burrowing. Apparently since abundant food is everywhere present (when the worms are living on the egg masses at least), the proboscis has become atrophied and is non-eversible.

The number of gonads in relation to body size is large. The testes are especially numerous. Internal fertilization and viviparity protect the

developing young for a longer time than would be the case if there were external fertilization only. The chances for each fertilized egg to reach maturity are thus increased.

### HOST DISTRIBUTION AND FREQUENCY ON PORTUNIDAE

A TOTAL of 334 ovigerous crabs was examined at the Museum of Comparative Zoology and at the United States National Museum. These included representatives of nearly all the large and commonly found families, except those which are terrestrial or fresh-water in habitat. Table 18 summarizes the results of the examination for Carcinonemertes.

Several hosts for the genus Carcinonemertes outside the family Portunidae have been reported. The complete list of non-portunid infestations is shown in Table 19.

A complete list of all the species of Portunidae now known to be infested with members of the genus Carcinonemertes is given in Table 20.

In all there are 27 species and subspecies of Brachyura (and probably one species of Anomura) known to be infested with Carcinonemertes. These nemerteans infest only those crabs with suitable ecological habits. According to Gerstaecker and Ortmann (1901, p. 1182), there are five ecological zones in which the Brachyura (and the Decapoda in general) live. They are the continental, fluvial, littoral, pelagic, and abyssal zones.

TABLE 18.—SUMMARY OF HOSTS EXAMINED AND INFESTATION FOUND IN MUSEUM MATERIAL

Family	Number of Species Examined	Number of Specimens Examined	Number In- fested with Carcino- nemertes
Euryalidae.....	1	1	...
Portunidae.....	53	204	29
Xanthidae.....	18	37	...
Majidae.....	22	41	...
Grapsidae.....	11	27	...
Dromiidae.....	2	2	...
Leucosiidae.....	2	2	...
Calappidae.....	5	6	...
Cancridae.....	3	6	...
Gecarcinidae.....	2	2	...
Goneplacidae.....	1	3	...
Galatheidæ*.....	1	3	...
<i>Totals</i> .....	121	334	29

\*This family belongs to the Anomura; the rest are Brachyura.



TABLE 19.—RECORDS OF INFESTATIONS BY CARCINONEMERTES OUTSIDE THE FAMILY PORTUNIDAE

Host	Family	Species	Author
<i>Galathea strigosa</i> Linnaeus . . .	Galatheidæ	? <i>C. c. carcinophila</i>	Dieck, 1874
<i>Xantho floridus</i> Mont. . . . .	Xanthidæ	<i>C. c. carcinophila</i>	Giard, 1888
<i>Pugettia producta</i> (Randall) . . .	Majidæ	<i>C. epialti</i>	Coe, 1902a
<i>Eriocheir japonicus</i> de Haan . . .	Grapsidæ	<i>C. mitsukurii</i>	Takakura, 1910
<i>Hepatus epheliticus</i> (Linnaeus)	Calappidæ	<i>C. c. imminuta</i>	Humes
<i>Persephona punctata</i>			
<i>aquilonaris</i> Rathbun . . . . .	Leucosiidæ	<i>C. c. imminuta</i>	Humes
<i>Panopeus herbstii</i> (Milne- Edwards) . . . . .	Xanthidæ	<i>C. c. imminuta</i>	Humes
<i>Menippe mercenaria</i> (Say) . . . .	Xanthidæ	<i>C. c. imminuta</i>	Humes

TABLE 20.—RECORDS OF INFESTATIONS BY CARCINONEMERTES IN THE FAMILY PORTUNIDAE

Host Crab	Species	Author
<i>Carcinides maenas</i> (Linnaeus) . . . . .	<i>C. c. carcinophila</i>	Van Beneden, 1861; McIntosh, 1869 and 1873-1874; Giard, 1888 and 1890; Joubin, 1890
<i>Callinectes sapidus</i> Rathbun . . . . .	<i>C. c. carcinophila</i>	Coker, 1901; De Turk, unpublished
	<i>C. c. imminuta</i>	Humes
<i>Callinectes ornatus</i> Ordway . . . . .	<i>C. c. carcinophila</i>	De Turk, unpublished
	<i>C. c. imminuta</i>	Humes
<i>Bathynectes superba</i> (Costa) . . . . .	<i>C. c. imminuta</i>	Pearse, unpublished
<i>Portunus spinimanus</i> Latreille . . . . .	<i>C. c. carcinophila</i>	De Turk, unpublished
<i>Ovalipes ocellatus ocellatus</i> (Herbst) . .	<i>C. c. carcinophila</i>	Coe, 1902a; Sumner, Osburn, and Cole, 1913; De Turk, unpublished; Humes
<i>Ovalipes ocellatus guadalupensis</i> (Saussure) . . . . .	<i>C. c. carcinophila</i>	De Turk, unpublished
<i>Portunus sayi</i> (Gibbes) . . . . .	<i>C. c. imminuta</i>	Humes
<i>Arenaeus cribrarius</i> (Lamarck) . . . . .	<i>C. c. imminuta</i>	Humes
<i>Portunus spinicarpus</i> (Stimpson) . . . .	<i>C. c. imminuta</i>	Humes
<i>Callinectes bocourti</i> M.-Edw. . . . .	<i>C. c. imminuta</i>	Humes
<i>Callinectes marginatus</i> M.-Edw. . . . .	<i>C. c. imminuta</i>	Humes
<i>Cronius ruber</i> (Lamarck) . . . . .	<i>C. c. imminuta</i>	Humes
<i>Callinectes danae</i> Smith . . . . .	<i>C. c. imminuta</i>	Humes
<i>Euphyllax dovii</i> Stimpson . . . . .	<i>C. epialti</i>	Humes
<i>Charybdis miles</i> de Haan . . . . .	<i>C. mitsukurii</i>	Humes
<i>Charybdis cruciata</i> (Herbst) . . . . .	<i>C. mitsukurii</i>	Humes
<i>Charybdis erythrodactyla</i> (Lamarck) . .	<i>C. mitsukurii</i>	Humes
<i>Portunus pelagicus</i> (Linnaeus) . . . . .	<i>C. mitsukurii</i>	Humes
<i>Charybdis natator</i> (Herbst) . . . . .	<i>C. coei</i>	Humes

Since Carcinonemertes will not live in air or fresh water, the crabs of the first two groups are eliminated as possible hosts. So far none of the abyssal crabs have been found infested. In such situations the crabs are not abundant enough and the conditions for transfer of the free-swimming larvae are unfavorable.

All of the species which have been thus far reported infested live in the littoral zone, with the possible exception of the one case reported above in the pelagic group, i.e., *Portunus sayi* (Gibbes), at Grand Isle, Louisiana. In that case, however, abnormal environmental factors brought about an infestation which was more or less accidental in character. For a month or more before the crab was collected offshore winds had been driving in great rafts of Sargassum or Gulf weed, upon which *P. sayi* lives. Much of this weed entered Barataria Bay through the passes and remained there for several weeks. On July 4, 1940, an adult female specimen of *P. sayi* was collected in Barataria Bay, just north of Grand Terre. One extremely minute specimen of *C. c. imminuta* was found on the gills. This worm, not exceeding 500  $\mu$  in length, was unfortunately lost. The writer believes that the presence of the worm on *P. sayi* was accidentally brought about by the unusually close contact between the latter and the numerous heavily infested *Callinectes sapidus*, which abounds everywhere in Barataria Bay and often crawls about in the Sargassum. All the specimens of *P. sayi* from other regions were uninfested.

All the infested crabs in Tables 19 and 20 live in depths less than 50 meters (i.e., they are omitted from Doflein's (1904, pp. 288-308) extensive list of Brachyura which live at depths greater than 50 meters or which in other words are deep-water species), with the exception of six species. These are *Xantho floridus* living at depths up to 77 meters, *Portunus spinimanus* to 97 meters, *Callinectes sapidus* to 143 meters, *Portunus spinicarpus* at 55 to 730 meters, *Portunus sayi* from the surface to 1084 meters, and *Bathynectes superba* from 100 to 1410 meters. All these six are littoral, however, in their distribution, and are rare at great depths.

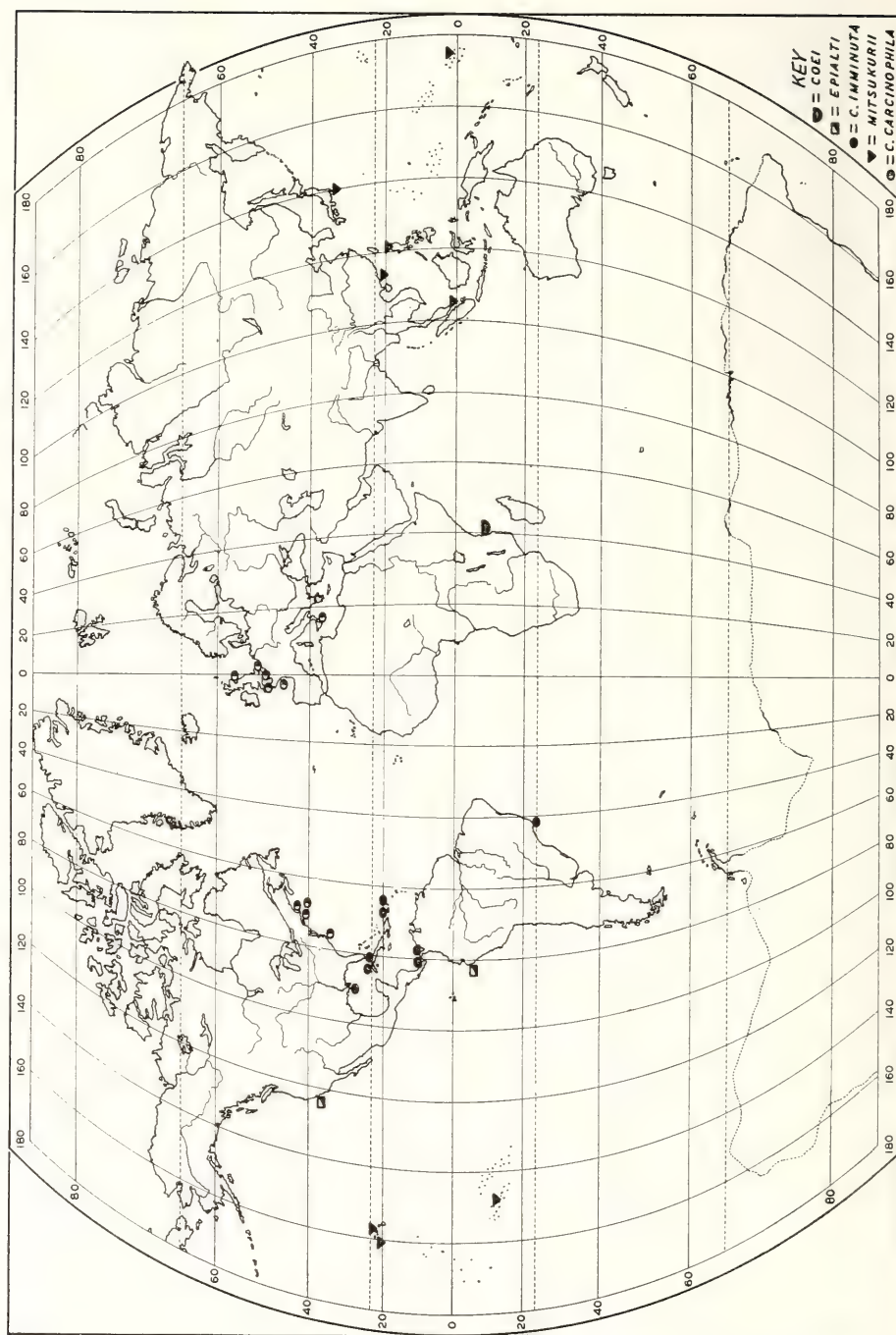
Certain conditions in the life habits of the littoral Portunidae make these crabs ideal hosts for members of the genus Carcinonemertes. In the first place, the littoral portunid crabs never leave the water, a habit of great advantage to the nemerteans, which dry rapidly in air. Incidentally this probably explains the extremely few infestations of zanthid and grapsid crabs, many of which often go about temporarily on land. Secondly, the portunids often swim about in the water, coming to the surface frequently. The positively phototactic free-swimming nemertean larvae seek the surface in response to the brighter light there. Thus the crabs and nemertean larvae are brought together, and the infestations

are begun. The fact that the entire family Majidae, the spider crabs, is, except for one species, *Pugettia producta*, uninfested is probably to be explained on the basis that these crabs do not swim to the surface and are therefore not brought in contact with the free-swimming larvae. In the third place, the habit of the Portunidae of swimming about actively tends to distribute the nemerteans over a large area, an important element in the survival and propagation of any animal which is closely dependent upon another for its existence. The rather stationary lives, in comparison, lived by the other littoral families of crabs (Xanthidae, Grapsidae, Majidae, and others) may account in part for their being uninfested. Lastly, the portunid crabs live in shallow waters and often occur in great numbers, so that, by the restriction of space and the shorter distance from hosts to host, infestations of new and reinfestation of old hosts are facilitated.

The general conclusion to be drawn is that normally the members of the genus *Carcinonemertes* infest the littoral Portunidae. In each case in which these nemerteans have been found upon other hosts, special features of the environment probably have acted to bring about such infestations. At Grand Isle, Louisiana, the presence of nemerteans on *Panopeus herbstii*, *Menippe mercenaria*, *Hepatus epheliticus*, and *Persephona punctata aquilonaris*, all non-portunid crabs, is believed by the writer to be caused by the extreme abundance of infested *Callinectes sapidus* in that area and by the unusually favorable conditions for the crabs to come in contact with the free-swimming larvae. The fact that the infestations on non-portunid crabs are always very light indicates that opportunities for their infestation are not as great as in the portunid crabs. In the four non-portunid species infested at Grand Isle the infestation never exceeded five worms on any one crab, and these were all minute, though some were sexually mature. It is likely that throughout the geographical range of the genus unusually heavy infestations may occur in areas which, like the Barataria Bay region, have abundant and suitable crabs and favorable conditions for the transfer of the free-swimming larvae to the host crabs. Where such heavy infestations occur, it is also likely that light infestations of some of the common non-portunid crabs may occur.

There does not seem to be much host specificity in the genus *Carcinonemertes*. The host on which the nemertean lives is infested not because there is some particular and necessary thing about that host which excludes all other crabs as possible hosts, but because the habits of that crab and the habits of the nemertean larvae are so interrelated that under suitable environmental conditions infestation is made possible. Whatever species of aquatic crab can fit into the already established life history of the nemerteans that crab is potentially a host for the worms. The portunid crabs, of all the Brachyura, meet the nemertean requirements most ideally.





## GEOGRAPHICAL DISTRIBUTION

THE MEMBERS of the genus *Carcinonemertes* are distributed in a wide belt around the earth between the tropic of Cancer and the tropic of Capricorn. The localities at which these nemerteans have been collected are shown on the map. The family *Portunidae*, on which the nemerteans chiefly occur, is of worldwide distribution in the littoral zone, and therefore offers opportunity for worldwide spread of the nemerteans.

*Carcinonemertes carcinophila carcinophila* (Kölliker) occurs at Messina, Sicily; Roscoff, Wimereux, and Concarneau, France; St. Andrews, Scotland; Ostende, Belgium; Beaufort, North Carolina; North Dennis and other regions south of Cape Cod, and Woods Hole, Massachusetts.

*Carcinonemertes carcinophila imminuta* has been found at Grand Isle, Louisiana; 10 to 20 miles south of the Tortugas, Florida; Fox Bay, Colon, Panama; Catano, San Juan Harbor, Puerto Rico; St. Thomas, West Indies, Porto Bello, Panama (Atlantic side); and Rio de Janeiro, Brazil.

*Carcinonemertes epialti* Coe is thus far known only from Monterey, California, and Payta, Peru.

*Carcinonemertes mitsukurii* Takakura has been collected at Yokohama Harbor, Japan; San Andreas Island, between Marinduque and Luzon, Philippine Islands; Hong Kong, China; Kauai, Hawaiian Islands; Apiang, Kingsmills Islands; Society Islands; Honolulu markets; and Singapore.

*Carcinonemertes coei* is thus far known only from Zanzibar, on the east coast of Africa.

## SUMMARY AND CONCLUSIONS

(1) *Carcinonemertes carcinophila carcinophila* (Kölliker) is recorded, on the basis of data supplied by Dr. Wm. E. De Turk, from four new hosts and a new locality.

(2) A new variety, *Carcinonemertes carcinophila imminuta*, found at Grand Isle, Louisiana, differs from *C. c. carcinophila* in its smaller size, shorter and more slender basis, and shorter stylet. A distinct sexual dimorphism in size and color is present. These worms reach sexual maturity at sizes much smaller than any previously known mature nemerteans.

(3) These worms crawl but cannot swim, nor can they fragment the body. Crawling worms are negatively phototactic, but the free-swimming larvae are positively phototactic.

(4) On the crab gills the nemerteans form capsules by cementing the two adjacent gill lamellae together around themselves. All worms on the egg masses of the crab, except the very minute ones, live in mucous,

lapilliform sheaths which they secrete and in the branches of which the females deposit their eggs.

(5) Cephalic muscle fibers are present along the rhynchodaeum and around the brain and esophagus. The anterior non-muscular part of the esophagus is capable of complete eversion, bringing the posterior muscular part outside the body where it acts as a sucking and pumping organ.

(6) The intestine in adult females has deep lateral pouches, but in males and worms with undifferentiated gonads the pouches are very shallow or absent.

(7) The proboscis is incapable of eversion. The basis measures 21 by  $5.3\ \mu$ , the stylet  $7\ \mu$  in length, and the ratio of stylet to basis is 0.352.

(8) The anal blood vessel and nerve commissures are both ventral to the posterior end of the intestine.

(9) The male reproductive system consists of testes, vasa efferentia, a mid-dorsal vas deferens, and a seminal vesicle. These canals, referred to as Takakura's duct, carry the spermatozoa from the testes to the lumen of the posterior end of the intestine. A thick ridge of cells of unknown function projects centrally from the mid-dorsal body wall and accompanies that part of the vas deferens anterior to the seminal vesicle. A translation of Takakura's (1910) description of this system in *Carcinonemertes mitsukurii* is presented.

(10) Early cleavage in *C. c. imminuta* is regular, equal, and probably of the spiral type. A ciliated free-swimming larva, slightly flattened dorso-ventrally, and bearing at each end a cirrus composed of several long, flagella-like elements, is formed.

(11) It is probable that the ciliated epithelium of the larva is not shed as claimed by earlier authors and that the only external change in the metamorphosis to a crawling worm is the loss of the cirri.

(12) The positive phototaxis of the larvae forces them to swim toward the surface where they come in contact with the crab host, *Callinectes sapidus*. Since immature crabs of both sexes and adult males molt relatively often, the nemerteans are unable to live long on them, being cast off at each ecdysis. Adult female crabs, however, do not molt, and this, together with the presence of eggs for food, makes infestation by nemerteans easy. The shallow water, comparative lack of strong currents, and the abundance of crabs all aid the larvae in coming in contact with new hosts in the Barataria Bay region.

(13) There is no correlation between the size of adult female crabs and infestation with nemerteans, or between the presence of nemerteans and the presence of the commensal barnacle *Octolasmis mülleri* (Coker).

(14) The worms migrate from the gills to the egg mass when the crab becomes ovigerous and back to the gills when the eggs of the crab



are hatched. Worms become sexually mature only on the egg masses of the crab. The gonads in worms on the gills are undeveloped. The nemerteans become sexually mature whenever the crab becomes ovigerous (in Louisiana from the last of March to the latter part of October). During cold weather, when the female crabs generally seek deeper water, the worms remain quiescent on the gills.

(15) The food of the nemerteans consists of the crab eggs. The effects of the worms on the crabs are slight. Free flow of water between the gill lamellae is prevented in heavy infestations, but heavily infested crabs appear to be just as vigorous as uninfested ones. No injuries to the gills were found, and it is improbable that the proboscis can be everted or that the stylet can pierce the chitinous covering of the gills.

(16) At Grand Isle, *C. c. imminuta* was found on eight species of crabs, six of them new host records for the genus. *Callinectes sapidus* is most commonly the host for these nemerteans in the Grand Isle region. On other crabs the nemerteans are small in size and few in number. Four other host crabs are reported from the West Indies and South America.

(17) A new host and locality for *Carcinonemertes epialti* Coe is reported.

(18) *Carcinonemertes mitsukurii* Takakura does not differ from *C. carcinophila* in the three respects that Takakura suggested, but does appear to differ in that the anal blood vessel commissure is dorsal instead of ventral to the posterior end of the intestine. Specimens which the writer believes should be temporarily at least assigned to *C. mitsukurii* were found on four new host crabs from new localities in the Pacific Ocean.

(19) A new species, *Carcinonemertes coei*, is described from *Charybdis natator* at Zanzibar. It differs from other species in its stouter body, the basis being swollen posteriorly, and having two rows of ovaries on each side of the intestine in the female.

(20) The family Carcinonemertidae, which name was first used by Sumner, Osburn, and Cole (1913), is re-established to include the single genus Carcinonemertes. The most important characteristics of the family are the presence of Takakura's duct, the much reduced proboscis with one central stylet and no accessory stylets or stylet pouches, the lack of cerebral sense organs, the massive development of the cephalic and sub-muscular glands, and the dependence upon crabs as a habitat. A key to the species and varieties is given.

(21) Although superficially the presence of Takakura's duct seems to indicate a relationship to the Acoela, the writer believes that this unique genital system is a separate development, independent of possible acoelan ancestry.

(22) The members of the genus *Carcinonemertes* are ectohabitants which feed upon the crab embryos, rather than ectoparasites.

(23) Of the 334 crabs examined in the collections of two museums, 29, all of them belonging to the family Portunidae, were infested with nemerteans. At the present time there are 26 species (one of which is divided into two subspecies) of *Brachyura* and 1 species of *Anomura* known to be infested with *Carcinonemertes*. Twenty out of the total of 27 brachyurans infested belong to the family Portunidae. Factors contributing to the high infestation of this family of crabs are (1) their wholly aquatic life, (2) their habit of swimming near the brightly lighted surface where the larvae of the nemerteans tend to collect, (3) their habit of swimming about actively, thus helping to distribute the worm larvae, and (4) their habit of living in shallow waters, often in great numbers, thus lessening the distance from host to host and increasing the chances for transfer of infestations. There is no host specificity in these nemerteans. The genus *Carcinonemertes* is distributed in the littoral zone in temperate and tropical seas around the world.

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## PLATES

All figures were drawn with the aid of a camera lucida, except figs. 5 and 51 which are free-hand sketches.

## PLATE I

- FIG. 1.—Mucous sheath of *C. mitsukurii* from egg mass of *Charybdis cruciata* at Hong Kong. Three crab eggs attached. Scale 1 mm.
- FIG. 2.—Mucous sheath of *C. epialti* from egg mass of *Euphylax dovii* at Payta, Peru. Scale 0.5 mm.
- FIG. 3.—Fragment of mucous sheath of *C. mitsukurii* from egg mass of *Charybdis erythrodactyla* from Society Islands. Scale 1 mm.
- FIG. 4.—Basis and stylet of *C. coei*. Drawn from a safranin-stained section. Scale 0.03 mm.
- FIG. 5.—Anterior cirrus of a free-swimming larva of *C. c. imminuta* showing its multipartite nature. Freehand sketch under oil immersion.
- FIG. 6.—Cross section of a lapillus and sheath of *C. c. imminuta*. Stained with Delafield's haematoxylin and eosin. Scale 0.1 mm.
- FIG. 7.—Anterior end of mucous sheath of *C. c. imminuta* from *Callinectes sapidus* at Grand Isle. A crab egg is shown beside the sheath. Scale 0.5 mm.
- FIG. 8.—Eight-celled stage of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 9.—Sketch of cephalic muscle fibers in region of rhynchodaeum in *C. mitsukurii*. The anterior end is directed toward the bottom of the drawing. Stained with Heidenhain's iron haematoxylin. Scale 0.05 mm.
- FIG. 10.—Four-celled stage of *C. c. imminuta*, lateral view. Scale 0.05 mm.
- FIG. 11.—Mucous sheath of *C. c. carcinophila* from *Ovalipes ocellatus* at Buzzard's Bay, Mass. Scale 1 mm.
- FIG. 12.—Posterior region of sheath shown in fig. 7. Same scale.
- FIG. 13.—Middle region of sheath shown in fig. 7. Same scale.



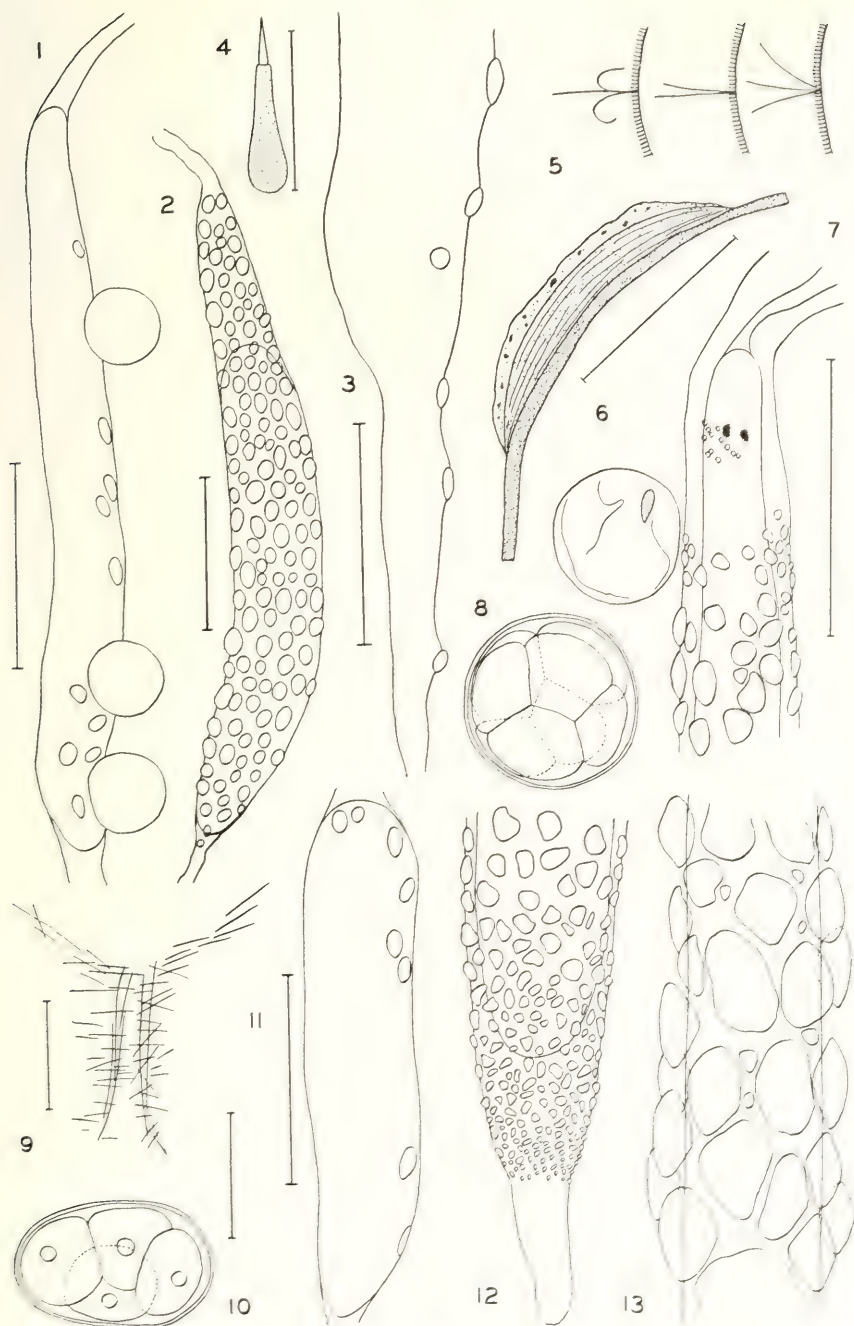


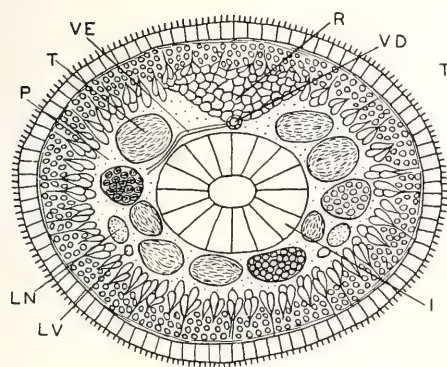
PLATE I

## PLATE II

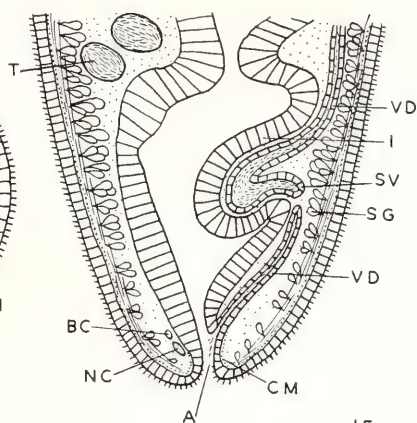
- FIG. 14.—Cross section of a mature male *C. c. imminuta* in the region of the vas deferens. Scale (upper one on plate) 0.1 mm.
- FIG. 15.—Sagittal section of the posterior end of a mature male *C. c. imminuta*. Scale (upper one on plate) 0.1 mm.
- FIG. 16.—Sagittal section of the anterior end of a mature *C. c. imminuta*. Scale (lower one on plate) 0.1 mm.
- FIG. 17.—Cross section of a mature female *C. c. imminuta* in the region of the ovaries. Scale (upper one on plate) 0.1 mm.
- FIG. 18.—Cross section of a mature male *C. c. imminuta* in the region of the seminal vesicle. Scale (lower one on plate) 0.1 mm.
- FIG. 19.—Cross section of a specimen of *C. c. imminuta* not sexually mature. Scale (upper one on plate) 0.1 mm.

## Abbreviations

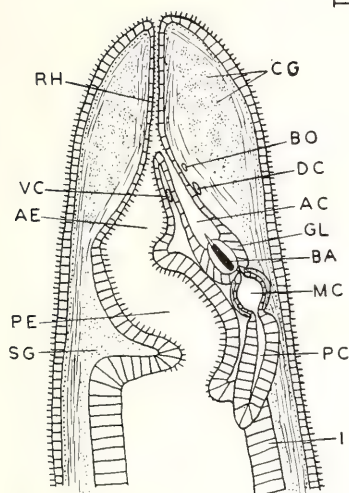
A.....anus	O.....egg
AC.....anterior proboscis chamber	P.....parenchyma
AE.....anterior part of esophagus	PC.....posterior proboscis chamber
BA.....basis	PE.....posterior part of esophagus
BC.....posterior blood vessel commissure	R.....ridge of cells along vas deferens
BO.....anterior blood vessel commissure	RH.....rhynchodaeum
CG.....cephalic glands	S.....spermatozoa
CM.....circular muscle fibers	SG.....submuscular glands
DC.....dorsal commissure of brain	SV.....seminal vesicle
GL.....gland cells in region of basis	T.....testis
I.....intestinal wall	VC.....ventral commissure of brain
IN.....integumental epithelium	VD.....vas deferens
LN.....lateral nerve cord	VE.....vas efferens
LV.....lateral blood vessel	W.....wall of ovary with developing eggs and yolk granules
MC.....middle proboscis chamber	
NC.....posterior nerve commissure	



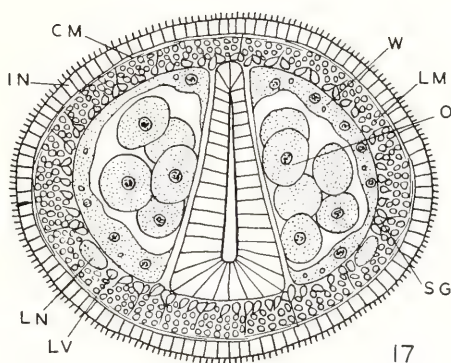
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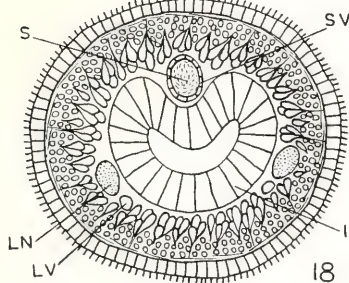
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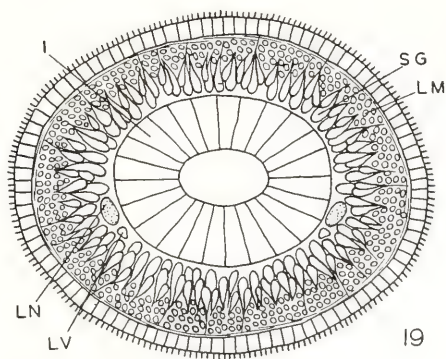
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PLATE II

## PLATE III

- FIG. 20.—Immature specimen of *C. c. imminuta*, 0.273 by 0.084 mm. Scale 0.05 mm.  
Abbreviations same as for Plate II, except for the following: *AB*, anterior blood vessel commissure; *B*, lobe of brain; *O*, ocellus; *ON*, ocellar nerve; *R*, rhynchodaeum; *S*, stylet.
- FIG. 21.—Part of an egg cord of *C. c. imminuta*. Scale 0.5 mm.
- FIG. 22.—Outline of a longitudinal section of a sexually mature female *C. c. imminuta*. Scale 2 mm.
- FIG. 23.—Outline of a longitudinal section of a sexually mature female *C. coei*. Scale same as for fig. 22.
- FIG. 24.—Mucous sheath of *C. epialti* from *Euphyllax doxii*. Scale 0.5 mm.
- FIG. 25.—Free-swimming larva of *C. c. imminuta*. Scale 0.05 mm.
- FIG. 26.—Arrangement of ovaries in a longitudinal section of *C. c. imminuta*. Scale same as for fig. 33.
- FIG. 27.—Outline of basis of *C. c. carcinophila*, as seen in section. Scale same as for fig. 31.
- FIG. 28.—Outline of basis of *C. epialti*, as seen in section. Scale same as for fig. 31.
- FIG. 29.—Outline of basis of *C. mitsukurii*, as seen in section. Scale same as for fig. 31.
- FIG. 30.—Cross section of basis of *C. c. imminuta*. Scale same as for fig. 31.
- FIG. 31.—Outline of basis of *C. c. imminuta*. Scale 0.02 mm.
- FIG. 32.—Mucous sheath of sexually mature female *C. c. imminuta*, 1.665 by 0.177 mm. Scale 0.5 mm.
- FIG. 33.—Arrangement of ovaries in longitudinal section of *C. coei*. Scale 0.6 mm.
- FIG. 34.—Smallest sexually mature female *C. c. imminuta* seen, 0.420 by 0.098 mm. Scale 0.2 mm.
- FIG. 35.—Mucous sheath of *C. coei* from *Charybdis natator* at Zanzibar. Scale 3 mm.



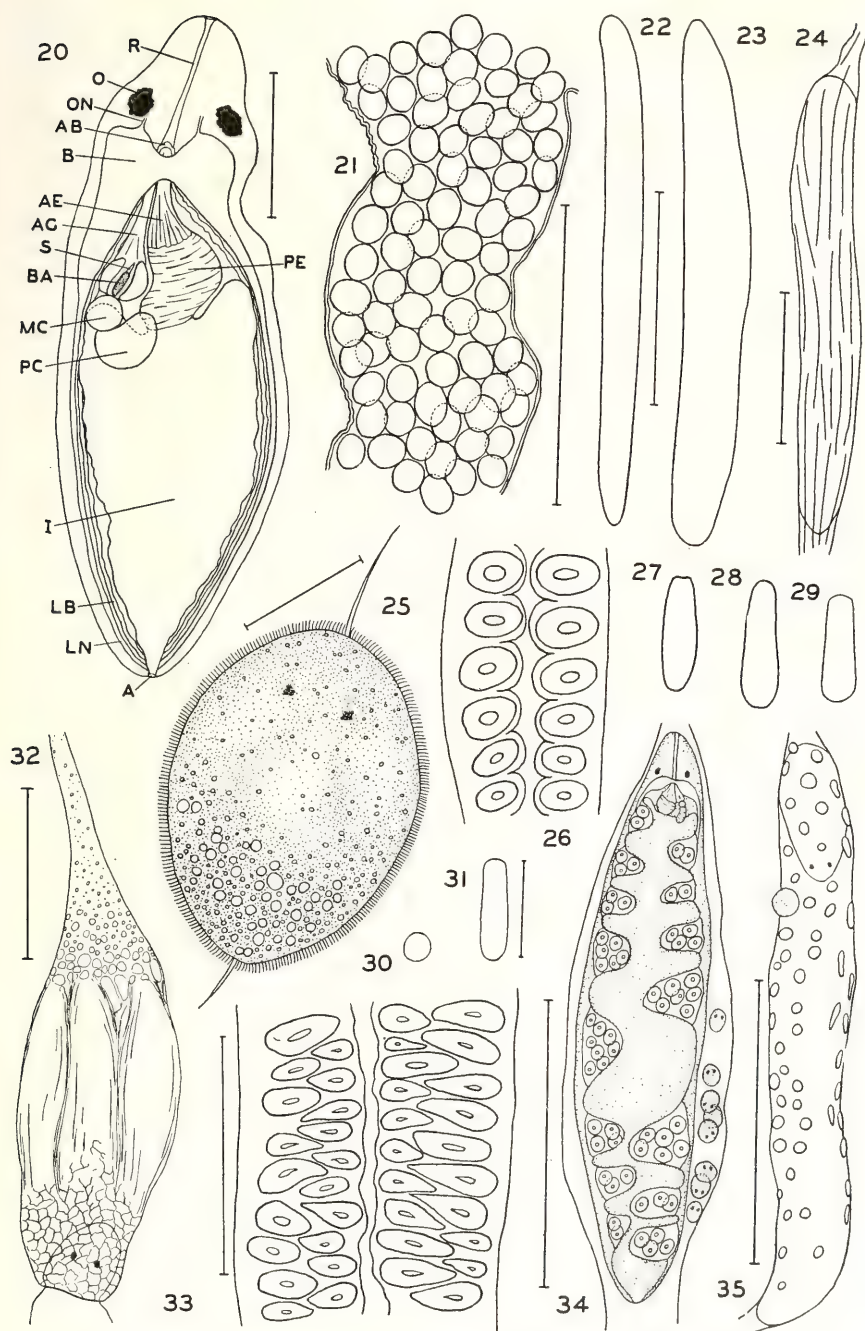


PLATE III

## PLATE IV

- FIG. 36.—Basis, stylet, and surrounding cells in *C. c. imminuta*. Scale 0.02 mm.
- FIG. 37.—Unfertilized egg of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 38.—One-celled stage of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 39.—Four-celled stage, polar view, of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 40.—Part of a cross section of an adult male *C. c. imminuta* in the region of the vas deferens. Treated with Feulgen's nucleal reaction. Scale 0.025 mm. Abbreviations same as for Plate II, except for the following: *L*, longitudinal muscle fiber; *S*, nucleus of submuscular gland cell.
- FIG. 41.—Part of a mucous sheath of *C. mitsukurii* from *Charybdis erythrodactyla* from the Society Islands. Scale 0.5 mm.
- FIG. 42.—Outline of the body of a living specimen of *C. c. imminuta*. Scale 5 mm.
- FIG. 43.—Basis and stylet of *C. c. imminuta* drawn from living worm. Scale 0.025 mm.
- FIG. 44.—Late embryo of *C. c. imminuta*, nearly ready to rupture egg membranes. Scale same as for fig. 10.
- FIG. 45.—Two-celled stage of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 46.—Blastula of *C. c. imminuta*. Scale same as for fig. 10.
- FIG. 47.—Contents of intestine of a living *C. c. imminuta* taken from a dark brown egg mass. Scale 0.05 mm.
- FIG. 48.—Dorsal view of the posterior end of an adult male *C. c. imminuta*. Scale 0.25 mm. Abbreviations same as for Plate II.
- FIG. 49.—Ovary of *C. c. imminuta* from which eggs have been shed. Scale 0.1 mm.
- FIG. 50.—Anterior end of *C. c. imminuta*, showing esophagus partly protruded. Scale 0.25 mm.
- FIG. 51.—A, B, and C are sketches of extruded esophagus of *C. c. imminuta*. The arrow shows the direction of peristaltic movements.
- FIG. 52.—Anterior end of *C. c. imminuta*, showing partly protruded esophagus. Scale same as for fig. 50. Abbreviations same as in Plates II and III.

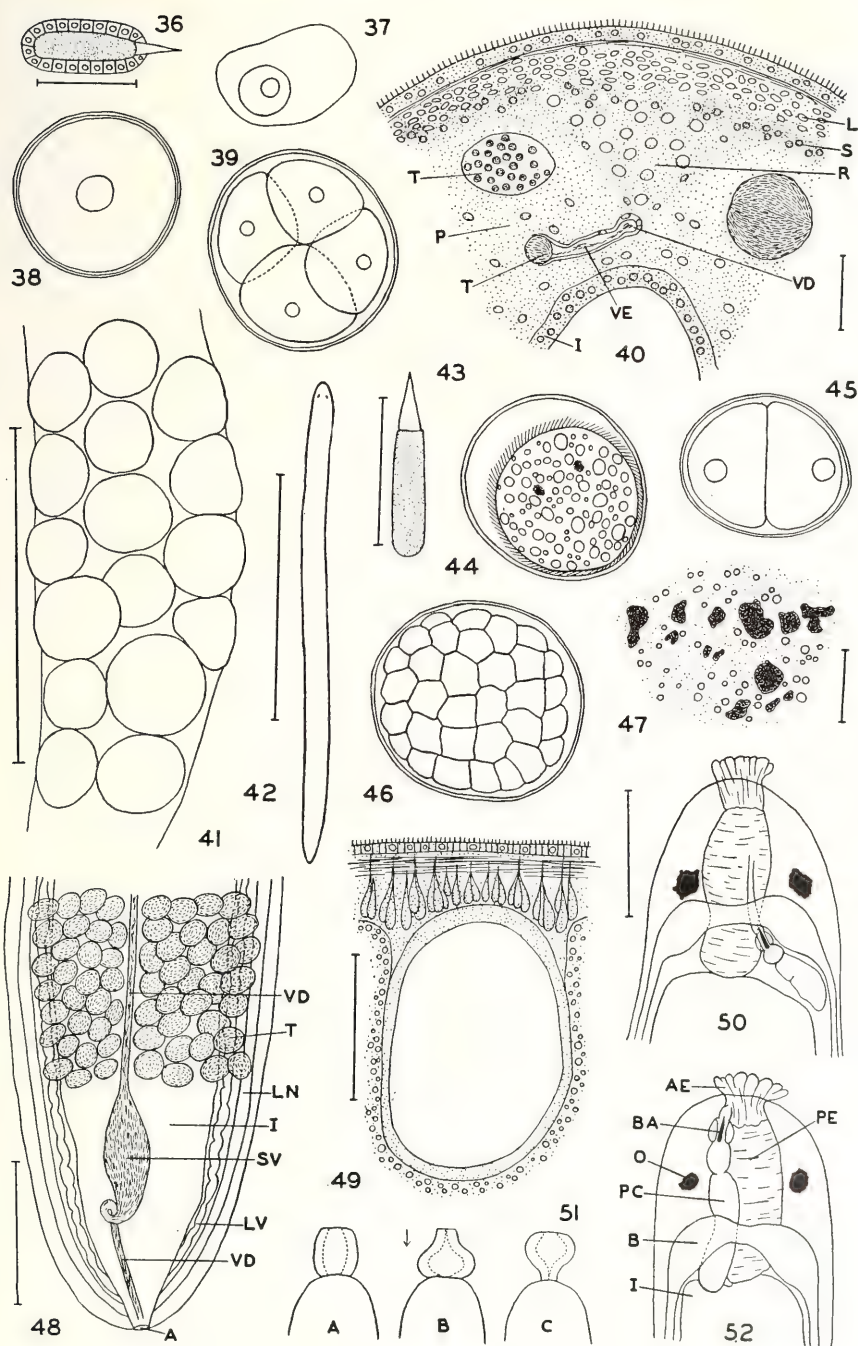


PLATE IV

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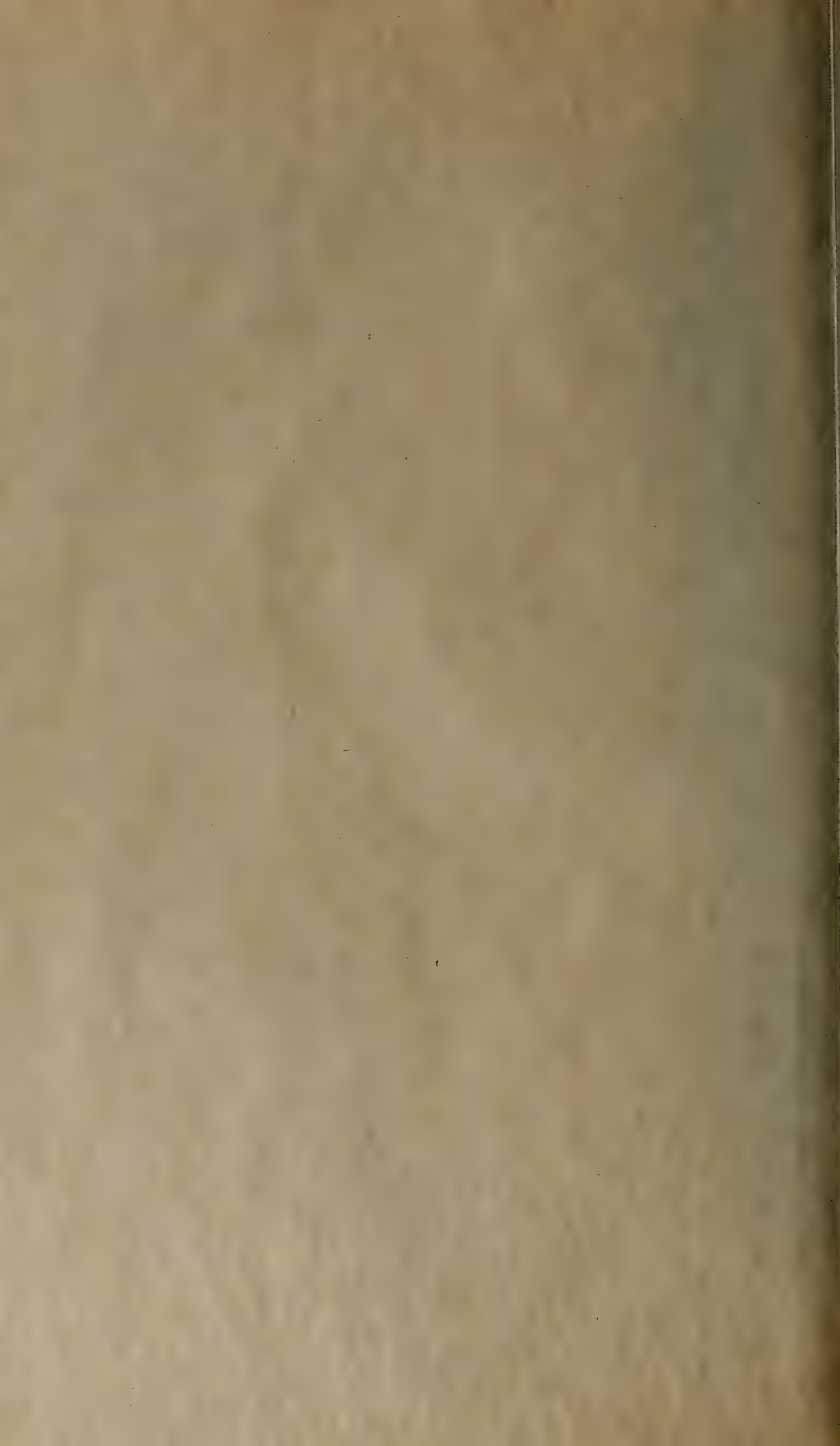
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